

Are Cochlear Implant Patients Suffering From Perceptual Dissonance?

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Cochlear implants provide functional hearing to the majority of recipients and have gained widespread acceptance clinically, but the range of performance remains great and largely unexplained. Designs for implanted electrodes and electronics have converged, whereas novel speech processing strategies have proliferated. For each patient, the fitting audiologist must sort empirically through options that produce large but idiosyncratic differences in both objective performance and subjective preference. This review and analysis suggests that the place-pitch and rate-pitch theories on which cochlear implants have been designed are incomplete. The missing component may be related to the phase-locking of auditory nerve activity to both acoustic and electrical stimulation. This component is likely to be highly distorted by electrical stimulation but its importance as one of several different pitch encoding mechanisms may vary widely among patients. Systematic means to control these putative phase effects using modern, high-speed, and high-density cochlear implants may make it possible to identify more efficiently the best strategy for a given patient and to minimize the perceptual confusion that arises from conflicting cues.

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The phrases “cognitive dissonance” and “perceptual dissonance” are commonly associated with general learning and musical intervals, respectively. They reflect more general phenomena, however, that may be applicable to understanding the perceptual difficulties faced by cochlear implant recipients. This paper considers the general problem of how conflicting cues tend to occur in various multimodal sensory tasks and how they are resolved normally by the brain. It hypothesizes that some cochlear implant recipients may have difficulty resolving conflicting cues about spectral information arising from the multiple ways in which such information is normally encoded by the temporospatial pattern of afferent activity and then decoded by the brain to recreate an internal representation of that spectral information.

The technology of cochlear implants in general has improved gradually but substantially over the past 20 yr. There has been a parallel overall im-

provement in the performance of patients on speech perception tasks. Individual performance, however, remains remarkably heterogeneous even within groups of patients who have few discernible differences in the cause or pathophysiology of their deafness or their responses to basic stimulation parameters (Dorman, Hannely, Dankowski, Smith, & McCandless, 1989; Dorman, Smith, & Parkin, 1996; Finley, Reference Note 11). Furthermore, there has been an unexpected divergence in the algorithms that postlinguistically deafened patients receive to convert acoustic information into temporospatial patterns of electrical stimulation in the cochlea. One explanation is that during their acoustic hearing period, these patients may have learned substantially different strategies for adjudicating among the many partially redundant cues whereby spoken words can be recognized. The relative importance of those cues may also be language specific (Xu et al., Reference Note 33).

Normally, a new class of medical devices starts out with several competing designs and then converges onto a preferred strategy embodied by all products with only minor variations. Hardware features of cochlear prostheses such as the implantation site and design of electrode arrays, the packaging of implanted, and external electronic components, and the transmission of data and power have, indeed, converged substantially since the 1980s. Improvements in functional performance, by contrast, have been achieved by providing an ever-growing range of strikingly different, software-based signal processing and stimulation strategies from which patients can choose even after they have received their implanted hardware (Wilson, Lawson, Muller, Tyler, & Kiefer, 2003; Wilson, 2000). The improvements in performance that have been achieved across the population of cochlear implant recipients may be related to improvements in the ability to test and match diverse speech processing strategies to diverse learned neural strategies for speech recognition.

The growing heterogeneity of ad hoc strategies and cognitive performance suggests that electrical stimulation produces unphysiological effects on a neural mechanism for pitch perception that is different from the place-pitch and rate-pitch mechanisms on which cochlear implants have been based (see below). This results in perceptual dissonance

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that subjects resolve in different ways. Until we identify and learn to control that unknown mechanism, the evolution of cochlear implants will remain frustratingly empirical and fragmented. Indeed, recent tests of new and "improved" strategies based on classic theories of auditory perception continue to confound predictions, producing inconsistent results at best (Cheng, Ishihava & Zeng, 2005; Blamey et al., Reference Note 2; Swanson, Blamey, McDermott, Patrick, Reference Note 29). This paper considers whether the missing component is a class of neural cross-correlators that extracts phase-locked activity in auditory neurons, as hypothesized by Loeb, White, & Merzenich (1983) to explain the unexpected psychophysical data then emerging from the first multichannel cochlear implant patients.

In an effort to relate my thesis to the most current experience and opinions regarding cochlear implants, I have cited work presented at the recent Conference on Implantable Auditory Prostheses in Asilomar, California, August 17 through 22, 2003 (<http://www.hei.org/ciap2005/ciap.htm>), supplemented with references and personal communications generously provided by many of the authors of those presentations. Interestingly, the summation presentation for this meeting concluded that "the most important unsolved problem in both acoustic and implant hearing is the coding mechanism for complex pitch" (Shannon, Reference Note 25).

Resolution of Conflicting Cues

The nervous system deals constantly with conflicting cues about external reality arising from the various sensory modalities. Such conflicts and their occasionally incorrect resolution provide the basis for virtually all of the sensory illusions that amuse both children and cognitive scientists. There are two basic approaches to resolving sensory conflicts: averaging them out or electing to rely on one information source at the expense of the others. In most situations, the approach appears to be hard-wired into the brain, but the specifics of how it is implemented can change over time as a result of natural learning, sensory pathology or structured rehabilitation. Here are examples of each approach.

Weighted Average • There are three distinct mechanisms for encoding and decoding the spatial origin of a familiar sound in extrapersonal space: interaural intensity difference, interaural time difference, and monaural spectral filtering of the sound by the convolutions of the pinna (Wightman, 1973). In an acoustically ideal world, these cues would always be aligned to create the same percept of spatial origin, but the real world is full of acoustic shadows and echoes and masking sounds that affect

these cues differently. By presenting synthesized acoustic information through headphones, it is possible to create cues whose conflicts are well controlled. Human subjects appear to take a weighted average of all three cues to arrive at a single approximation of the sound source, even when the perceived origin may not agree with any of the individual cues (Macpherson and Middlebrooks, 2002). Other examples of weighted averaging have been described for the combination of visual and proprioceptive feedback in motor planning (Sober, & Sabes, 2003). Interestingly, the motor behavior suggests that subjects are able to use different weighting factors for different phases of a given task.

Winner Take All • There are three distinct mechanisms for encoding and decoding the relative motion of the body with respect to the world (a key component of our overall sense of balance): acceleration of the head as detected by the vestibular system, optical flow as sensed by the eyes, and angular motion of the joints as detected by proprioceptors (particularly muscle spindles) (Nashner, 1980; Nashner, Woollacott, & Tuma, 1979). These senses differ in the speed and precision of their information and susceptibility to false cues. It is easy experimentally to generate a conflicting cue in one of the three sensory modalities and to ask subjects about their sensations (or to observe their reflexive postural adjustments as the brain attempts to maintain postural stability). Such experiments demonstrate that normal human subjects usually rely exclusively on vestibular information, completely suppressing conflicting cues from the other two systems (McCullum, Horak, & Nashner, 1984). Patients who have sustained damage to the vestibular apparatus, even damage of which they are essentially unaware, tend to rely instead on optical flow signals (Creath, Kiemel, Horak, & Jeka, 2002). This may result in disconcerting problems in naturally conflicted situations such as moving vehicular traffic. Such patients can actually be taught to ignore visual cues in favor of proprioceptive cues to improve their overall performance in such situations (Shumway-Cook, & Horak, 1990; Fay Horak, personal communication).

Mechanisms for Encoding and Decoding Pitch

Mechanisms for encoding pitch can be identified by examining temporospatial patterns of activity in the population of cochlear nerve activity. This has resulted in three generally accepted and essentially orthogonal encoding mechanisms: place-pitch, rate pitch, and a poorly understood "phase-locked" pitch. The latter two are sometimes lumped into the con-

cept of “temporal pitch” (e.g., Wouters et al., Reference Note 32) or “fine structure” (e.g., Zeng et al., Reference Note 35), but there is much evidence for two separate mechanisms in both acoustic and prosthetic hearing.

It is important to remember that the identification of a pitch encoding mechanism in the afferent signals does not mean that there is a corresponding central decoder for that putative cue. Teleologically, it seems that there should be, but it may not be possible for neurons to decode some cues, particularly when they involve temporal features that are much faster than the biophysical processes of action potentials and synaptic transmission. Furthermore, human speech contains many redundant cues, so that even highly impoverished representations tend to be intelligible (Dudley, 1939; Fletcher, & Galt, 1950; Hill, McRae, & McClellan, 1968). The three encoding mechanisms summarized below are believed to be associated with some central decoding mechanism because they seem necessary to account for the results of psychophysical experiments on auditory perception.

Place pitch, based on the spectral filtering properties of the basilar membrane, operates over the entire range of audible frequencies but has substantial problems with accuracy and precision over the wide dynamic range of sound intensity and perceived loudness. That is because the spatial filters are highly nonlinear and asymmetrical. Neural spike activity tends to saturate and its distribution shifts basally as the amplitude of a single tone increases. If two closely spaced frequencies are presented together, there are distortion products in the basilar membrane motion and nonlinear summation in the neural activity. Somehow the brain corrects for this distortion or suppresses the inaccurate information entirely to give rise to the remarkable constancy of pitch perception over a very wide dynamic range of loudness and musical intervals (Olson, 1966; see below).

Rate pitch is akin to the sense of tactile vibration. It operates only at frequencies for which individual neurons can generate cycle-by-cycle action potentials, a capability that declines sharply in the auditory nervous system above 300 to 500 Hz (Rose, 1970). However, rate information probably is encoded and decoded from everywhere along the basilar membrane because most naturally occurring acoustic sources are composed of overtones of fundamental frequencies that lie within the rate pitch range. The envelope of the higher overtones tends to be amplitude modulated at the fundamental frequency. The pitch ascribed to an electrical stimulation train by a cochlear implant subject tends to be related to the frequency of stimulation at low fre-

quencies (100 pps) but becomes dominated by place of stimulation at ≥ 300 pps (Zeng, 2002).

Phase-locked pitch is an encoding mechanism in search of a decoding mechanism (reviewed in Loeb, White, & Merzenich, 1983). Over the entire frequency range that is critical for speech perception (300 to 3000 Hz), auditory neurons tend to generate their action potentials in phase with basilar membrane motion but at random subharmonics that lie within their limited range of firing rates (Anderson, Rose, Hind, & Brugge, 1971; Fig. 4.7 in Kiang, 1965). By combining the trains of action potentials from an ensemble of such phase-locked neurons at a single location on the basilar membrane, the frequency of pitches well above the rate-pitch range could be represented in the frequency of the composite “volley” of action potentials (Wever, 1949). Several acoustical psychophysical phenomena suggest that the phase-locked signal is actually used to provide pitch information (reviewed by Loeb, White, & Merzenich, 1983), but it is not clear how this signal is decoded by the central auditory nuclei.

Putative Mechanisms for Decoding Phase-Locked Pitch

Temporal autocorrelation of the volley was proposed as a decoding mechanism for phase-locked pitch: multiplicative recombination of the original spike train with the same spike train delayed by the period of the frequency to be detected (Licklider, 1951). Paradoxically, however, cochlear implant recipients do not perceive pitches related to the frequency of stimulation above 300 Hz (Eddington, Dobelle, Brackmann, Mladejovsky, & Parkin, 1978; Zeng, 2002; Chen, & Zeng, Reference Note 7), even when those frequencies are applied near the appropriate cochlear place (McKay, McDermott, & Carlyon, 2000). Electrical stimulation produces particularly strong phase-locking of neural activity, as recorded from single units in recently deafened animals (Litvak, Delgutte, & Eddington, 2001; Loeb, White, & Jenkins, 1983; Van Den Honert, & Stypulkowski, 1987) and as evoked potentials in cochlear implant patients (Wilson, Finley, Lawson, & Zerbi, 1997). This implies that the decoder of the phase-locked information must employ an algorithm different from temporal autocorrelation (Zeng, 2002). Some form of spatial cross-correlation would appear to be necessary (Loeb, White, & Merzenich, 1983). When a single tone is presented at sufficient intensity, phase-locking will occur over a substantial length of the cochlea; the trains of action potentials will exhibit a coherent spatial gradient of relative phasing that results from the traveling wave properties of the basilar membrane (see below). Recently,

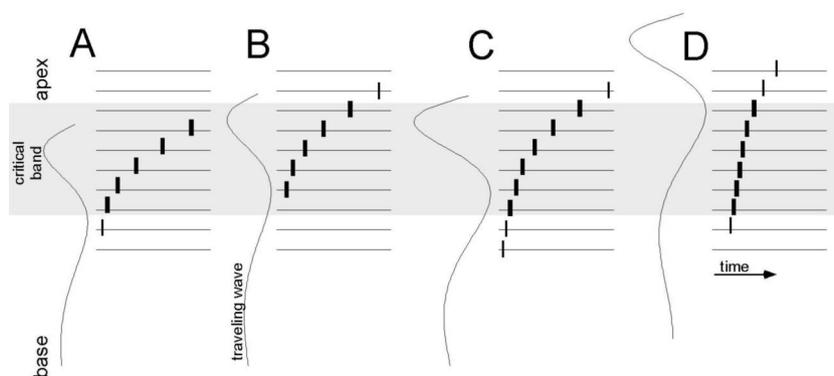


Fig. 1. Schematic representation of the phasing of neural unit activity (horizontal axes = time, arrow corresponds to $250 \mu\text{sec}$) as a function of distance along the cochlea (vertical axis, upward = apical, total length represented 3 mm). (A) Traveling wave associated with a single acoustic frequency whose place of resonant tuning corresponds to the light gray “critical band” over which a putative neural detector extracts the phase relationship among arriving action potentials (identified by thick bars). (B) Slightly lower frequency than A. C, Same frequency as B but twice the amplitude. D, Much lower frequency than A at twice the amplitude. See Shamma (1985a) for detailed simulations based on traveling wave mechanics and neural transduction.

acoustic phase-locking of neural activity has been used as a tool to produce a detailed map of the amplitude, velocity and phasing of traveling wave propagation at various sound intensities over the entire extent of the cat cochlea (van der Heijden, & Joris, 2003).

The wavelength of a traveling wave depends on both its frequency and its proximity to the region of resonant tuning, where velocity slows greatly as the amplitude increases and then dies out abruptly (Pfeiffer, & Kim, 1975; reviewed by Robles, & Ruggero, 2001). Little attention has been paid to this feature, but it may well be more phylogenetically salient than the Helmholtzian focus on the amplitude peak at the resonant place.

It seems likely that the auditory system evolved first to maximize sensitivity to weak sounds that produced weak but coherent motion over an extended receptor surface like the basilar membrane (or its predecessor, the lateral line organ of fish). The usual neural mechanisms to amplify such coherence by spatial integration (i.e., interneuronal networks such as used for surround inhibition) will not work at acoustic frequencies >300 Hz because synaptic potentials last for many milliseconds. The problem was overcome by active mechanical gain from large numbers of independent high-frequency actuators, i.e., outer hair cells (Dallos et al., 1997; Hudspeth, 1989). The acoustic input provides a weak but coherent input signal across a population of outer hair cells that are otherwise driven by incoherent Brownian noise. The net mechanical activity of the population tends to distort as well as to amplify and focus the incident mechanical waveform that is responsible for this coherence (Kim, Molnar, & Matthews, 1980), creating rich temporospatial patterns to be transduced and detected by the neural decoders.

In the highly evolved mammalian cochlea with its systematic gradient of mechanical properties, coherent mechanical amplification by the outer hair cells results in the abrupt slowing of the traveling wave at the point of resonant tuning. As depicted schematically in Figure 1A, spiral ganglion cells that are phase-locked to basilar membrane motion will have the steepest and most rapidly changing spatial gradient of phase for the locally resonant frequency (Loeb, White, & Merzenich, 1983; Shamma, 1985a). Much shallower and more constant phase gradients will occur at the same location for lower frequencies that have sufficient amplitude to excite these ganglion cells as they pass through to their more apical tuning point (Fig. 1, B through D). Increases in acoustic amplitude of a given frequency tend to saturate the firing rates of ganglion cells from progressively larger regions extending basally but they do not change the phase gradients (Fig. 1, B and C) (Kim et al., 1980). Closely spaced harmonics tend not to be resolvable based on mean firing rates at moderate loudness, whereas abrupt phase transitions persist at the resonant place for each harmonic (Shamma, 1985a). These phase shifts persist even when the adjacent harmonics are more intense and dominate the phase-locking itself. If the local phase gradient could be extracted from the phase-locked discharge of the spiral ganglion cells, it would provide the information required to account for the remarkable stability of pitch versus loudness at frequencies approximately 1 to 3 kHz (p. 251 in Olson, 1966) and for the otherwise paradoxical improvement in frequency discrimination with increasing loudness (Wier and Green, 1976).

The details and even the existence of the putative neural decoder of pitch from phase-locked neural activity remain hypothetical, but some inferences can be drawn from physiology and psychophysics

(Loeb, White, & Merzenich, 1983). When multiple, closely spaced acoustic frequencies are combined on the basilar membrane, the regions of phase-locking to a single frequency tend to be about one critical band long (1 mm; Sachs, & Young, 1980), which corresponds to the smallest frequency spacing that is perceived as a musical interval rather than as timbre when two notes are played simultaneously (the major second; two semitones). Thus, it seems likely that the phase-locked pitch decoding mechanism operates over basilar membrane distances ≤ 1 mm but long enough to experience a substantial phase gradient (at least 90° ; Loeb, White, & Merzenich, 1983). This relatively short distance would account for the absence of discernible effects from changes in the sequencing of stimulation in multichannel cochlear implants (i.e., basal-to-apical, reversed or random; Blamey et al., Reference Note 2). Even the closest spaced electrodes (0.8 mm in Nucleus implants) are near the limits of spatial cross-correlation and such electrodes produce massive channel interaction when adjacent contacts are activated even in an interleaved temporal pattern (Bierer, & Middlebrooks, 2004; Shannon, 1983; Eddington et al., Reference Note 10).

The neural decoder could operate as an ensemble of short-distance cross-correlators covering the range of phase-locked frequencies (300 to 3000 Hz). By including delays, inhibitory synapses, or local dendritic circuits for synaptic gating, it is possible to create ensembles that represent component pitches as peaks, valleys, edges, and so forth, in the neural population (e.g., Shamma, 1985b). From the detailed patterns computed by Shamma (1985a; illustrated schematically in Fig. 1), one of the most salient cues appears to be the second derivative of phase. At the characteristic place (Fig. 1A), a tonal stimulus would result in a convergence of high levels of neural activity (to be decoded as place pitch) and maximal phase acceleration (to be decoded as phase-locked pitch). A slightly lower pitched tonal stimulus with high loudness (Fig. 1C) would produce similar place-related activity (because of saturation) but would have a significantly lower phase acceleration over this range of CFs. A much lower pitched tonal stimulus (Fig. 1D) might produce a much flatter phase gradient but the nervous system might not use this information to influence pitch judgment because its place pitch is located much more apically.

Whatever patterns are actually extracted by the ensemble of cross-correlators will always be closely related to the pitches that could be extracted by a simple place-pitch decoder for the corresponding pure tones. This makes it feasible for the nervous system to learn associations during the development

of speech and hearing. Conversely, this tendency makes it virtually impossible to test hypotheses about phase-pitch extraction using acoustic stimuli and psychophysical measurements. A similar problem has been noted for rate-pitch experiments (Oxenham, Bernstein, & Penagos, 2004). If the nervous system does, indeed, learn these associations rather than having them wired in genetically, this has important implications for congenitally deaf recipients of cochlear implants. In particular, some of the experiments suggested below may produce different results in such patients (although they may lack the vocabulary to describe their percepts in the same way as postlinguistically deafened patients).

Pitch Encoding by Cochlear Implants Using CIS Strategy

It seems likely that the rather crude electroneural interface offered by a cochlear implant introduces substantial distortions into all three of the neural cues for pitch. These distortions are likely to be different from those that arise and are normally easily resolved in acoustic hearing (e.g., pitch constancy with loudness as discussed above; various distortion products, Robles, & Ruggero, 2001). The central question raised here is how does the central nervous system resolve perceptual conflicts that may arise among these cues in both acoustic and prosthetic hearing. Are the cues averaged to determine a single representation of the spectral space, does one cue dominate and occlude the others, or are there separate, parallel representations giving rise to a sense of relative consonance versus dissonance (e.g., timbre) as well as net pitch? These are questions that are difficult, if not impossible, to resolve using acoustic stimuli because the mechanics of the basilar membrane force the cues to covary. Can we use the unique distortions produced by cochlear implants as a tool to answer these questions?

All modern, multichannel cochlear implants seek to provide spectral information about pitch by tonotopic stimulation of the spiral ganglion with amplitudes related to the energy in the corresponding frequency bands of the acoustic signal. Electrical stimulation at a given place in the cochlea produces sound percepts that have a distinct pitch related to the place, but they are not reported as tonelike regardless of stimulus parameters (Eddington et al., 1978). This may reflect a mismatch between the place cues and phasing patterns produced by electrical stimuli, as explained below. Nevertheless, the auditory nervous system seems to be able to extract spectral information about speech sounds equally from the unnatural percepts elicited by electrical stimulation as well as acoustic pure tones (Hill et

al., 1968) and acoustic band-limited noise, despite very different temporospatial patterns of neural activity. All three representations can produce understandable speech with only four separate channels of information distributed across the speech frequencies (Fu, Shannon, & Wang, 1998) and modulated at subacoustic rates (Fu, & Shannon, 2000).

Attempts to encode rate pitch by systematically varying the frequency of electrical stimulation (pulsatile or sinusoidal) produce confusing results. Cochlear implant recipients can be persuaded to estimate overall pitch in a way that suggests that rate pitch modulates the place pitch (Eddington et al., 1978; Zeng, 2002; Chen, & Zeng, Reference Note 7), but this does not mean that they hear a single, coherent sound with the estimated pitch. These data are also consistent with the notion that the subjects are hearing two distinct sounds with incompatible pitches, which they can suppress, use, or combine depending on what provides useful information for the task at hand (McKay, McDermott, & Carlyon, 2000; Tong, Dowell, Blamey, & Clark, 1983; Carlyon, Long, & Deeks, Reference Note 5; Fridman, Reference Note 12; Galvin, & Fu, Reference Note 14; Laneau, Moonen, & Wouters, Reference Note 17).

Most cochlear implants now use variants of the continuous interleaved sampling (CIS) strategy (Wilson et al., 1991). Biphasic pulses are delivered to only one electrode at a time; local neurons are either excited to threshold by the cathodic phase or returned to resting depolarization by the subsequent anodic phase. This reduces cross-talk between adjacent channels, improving the resolution of place-pitch. The repetition rate on each electrode is set high enough to produce no rate-pitch sensation. Recently, much higher rates have been used in speech processors that are still identified as CIS, but as we shall see later, these probably work on very different biophysical principles that would be expected to have substantial perceptual consequences.

Early attempts to represent the pitch of the voiced fundamental in the repetition rate of pulsatile stimuli produced information that was useful for identifying sounds that differed in low frequency pitch (e.g., male versus female speaker identification; Tong, Clark, Seligman, & Patrick, 1980). It was not particularly useful for identifying speech sounds; indeed, the brain presumably learns to generalize semantic information across speakers largely by ignoring the rate-pitch information. Substantially higher but fixed repetition rates result in improved speech perception. One hypothesis to account for this improvement with stimulation rate is that the higher rates improve the fidelity of the representation of envelope modulation by avoiding the false cues that arise when lower frequency pulse

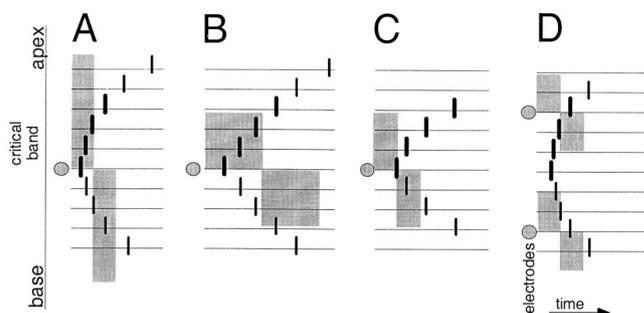


Fig. 2. Schematic representation of the phasing of neural unit activity similar to Figure 1 (vertical axis = place, extent 2 mm; horizontal axis = time, arrow 250 μ sec). A, Activity evoked by a moderately short biphasic pulse (e.g., 70 μ sec/phase). B, Activity evoked by a long biphasic pulse (e.g., 250 μ sec/phase) with the same intensity as A (product of amplitude times duration). C, Half the intensity of A and B (duration similar to A, amplitude similar to B). D, Virtual channel created by simultaneous stimuli on two adjacent electrode contacts.

trains beat against the envelope modulation frequencies and the refractory periods of the neurons (Wilson et al., 1997). Nevertheless, even when the stimulation rates are high enough to permit an accurate representation of envelope modulation in the phase-locked pitch range (300 to 3000 Hz), no corresponding sensation of pitch is perceived (Carlyon, & Deeks, 2002; Carlyon, van Wieringen, Long, Deeks, & Wouters, 2002; Landsberger, & McKay, Reference Note 16; Shannon, Reference Note 25).

Phase Gradients Induced by Pulsatile Stimulation

There have been no systematic attempts to represent phase-locked pitch information electrically. Nevertheless, electrical stimulation inevitably produces strong phase-locking of evoked action potentials (Litvak et al., 2001; Loeb, White, & Jenkins, 1983; Van Den Honert, & Stypulkowski, 1987; Wilson et al., 1997). Furthermore, it is likely that electrical stimulation produces gradients of phase-locking over approximately the same spatial range across which pitch extraction by spatial cross-correlation is likely to operate, namely, a critical band (1 mm). That is because the spiral ganglion cells closest to the stimulating electrode will tend to have the lowest threshold for excitation by a stimulation pulse. A pulse that is above threshold for all of the neurons in a critical band will elicit action potentials with a systematically longer latency on either side of the stimulating electrode (Fig. 2). The analysis that follows considers this from the perspective of a single neuron responding to idealized monopolar, monophasic stimulation. The effects produced in a population of spiral ganglion cells by a clinical

prosthesis are subject to additional factors, including heterogeneity of the neurons and bipolar electrode configurations producing mixed cathodal and anodal effects. Such effects include slowing from anodal hyperpolarization, creation of virtual cathodes around anodes, and shifts in the site of spike initiation (between apical dendrite and axon hillock).

From biophysics, we can identify two mechanisms that should determine the shape and coherence of the latency gradient produced by electrical stimuli. The first is the tendency of any neural cell membrane to act as an integrator for the transmembrane current induced by each phase of the stimulus (Ranck, 1975). Consider a stimulus pulse that is strong enough to produce depolarizations that exceed threshold in a spatially extended but otherwise homogeneous population of neurons. The neurons closest to the stimulus source will be subjected to a stronger potential gradient that produces higher transmembrane currents that will reach threshold early in the pulse; those further away will fire progressively later in the pulse. By independently adjusting pulse amplitude and width, it is possible to create two pulses with different durations that excite the same population of neurons but create two different latency gradients (compare Fig. 2A and Fig. 2B). A second mechanism affects the latency in the population of neurons near the fringes of the excited region, which are depolarized near threshold. It arises from the stochastic nature of the thermodynamics of voltage-dependent sodium channels, which do not all open abruptly at the same membrane potential (Crago, Peckham, Mortimer, & Van der Meulen, 1974). If only a few of the channels open, their inward sodium current can add to the depolarization produced by the stimulus pulse itself and gradually push the remaining channels open, but the eventual action potential will be much delayed. This gives rise to the similarly large gradients in latency shown at the fringes of the populations of excited neurons for all stimuli depicted in Figure 2.

Perceptual effects in cochlear implant patients have been ascribed to the above-described latency gradients. Dobie and Dillier (1985) reported that trapezoidal pulses with rise times as short as 80 μ sec could be distinguished from square waves by Ineraid implant patients and suggested that the mechanism involved relative synchrony of auditory neurons. Some but not all recipients of the CLARION implant have strong subjective preferences for the sinusoidal stimulation of compressed analog speech processors (Battmer, Reid, & Lenarz, 1997) compared with interleaved pulse strategies, which would tend to produce more locally synchronous neural activity. Substantial variability among sub-

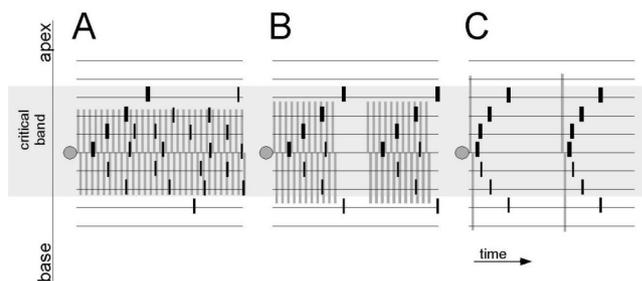


Fig. 3. Schematic representation of the phasing of neural unit activity similar to Figure 2 (vertical axis = place, extent 2 mm; horizontal axis = time, arrow 250 μ sec). Stimulus amplitudes adjusted to produce equal extent of firing and equal loudness in all panels. **A**, High frequency train of very short biphasic pulses (e.g., 10- μ sec/phase at 20 kHz); note that there is a coherent phase at the start of the train but it rapidly randomizes if the train is continuous. **B**, Same high frequency carrier as **A** but divided into bursts; note recurrence of phase gradient in each burst. **C**, Individual biphasic pulses at the same rate as the burst frequency in **B**; note high acceleration of phase gradient.

jects would be expected because the spiral ganglion cells of cochlear implant recipients are not, in fact, homogeneous (Spoendlin, 1979). Their underlying disease process may produce substantial heterogeneity in the histology and electrical properties of the surviving cells, which will tend to disrupt the orderly gradients of latency depicted schematically in Figures 2 and 3.

The phase gradients that result from electrical stimulation seem likely to activate the phase-locked pitch extraction circuitry, but in highly unphysiological ways whose effects are difficult to predict. By comparing the phase-gradients associated with acoustic stimuli in Figure 1 with those depicted in Figures 2 and 3, we can speculate on how the nervous system might attempt to estimate a single pitch from the two different cues of place and phase. The phase gradients produced by electrical stimulation will tend to be symmetrical around the electrode in the basal and apical directions, but there are likely to be neural decoders only for the apically directed gradients because basally directed gradients cannot arise from traveling wave mechanics. As we saw in Figure 1, gradients that are steep and accelerating rapidly signify agreement between place- and phase-locked pitch; gradients that are flat are associated with apically tuned, hence lower pitched acoustic stimuli.

Figure 2A shows a relatively short but strong stimulus pulse, which produces a shallow gradient in the neurons near the electrode, for which the stimulus is well above threshold, plus an accelerating phase gradient in the "tail" of more distant

neurons that are near threshold. Figure 2B shows an equally strong pulse composed from a lower amplitude but longer duration. This produces a steeper phase gradient in the strongly recruited neurons (compared with Fig. 2A) because the neurons further from the electrode reach threshold and fire nearer to the end of the long stimulus pulse. The recruited population also has a tail with further phase delays in neurons that are depolarized near threshold, but there will be less acceleration of phase between the region where neurons are depolarized well-over threshold and the region where neurons are firing near threshold. Figure 2C shows a weak stimulus with a short duration, which shifts the region of phase acceleration (i.e., neurons near threshold) closer to the center of stimulation, putting it within the critical band over which place- and phase-pitch information are expected to interact perceptually. The situation for virtual channels (overlapping stimulation on adjacent electrodes, Figure 2D, see text below) is more complex. For the simple situation illustrated, we might expect a fairly flat phase gradient between the electrodes and rapid acceleration at the edges, which are near threshold. All of these examples are offered merely to illustrate general principles; the interactions among stimulus parameters, electrode placement and condition of the spiral ganglion cells are likely to be highly nonlinear and will require systematic modeling to elucidate (see below).

Interestingly, when unmodulated, loudness-matched pulse trains are delivered over a range of high frequencies that is entirely above the rate-pitch range, subjects can distinguish different frequencies but do so by percepts perhaps related to timbre (see below) rather than pitch (Shannon, 1992; Landsberger, & McKay, Reference Note 16). The slopes of the phase gradients associated with such stimuli will depend complexly on the pulse width (Fig. 2A versus Fig. 2B), the relationship of stimulus intensity to threshold (Fig. 2B versus Fig. 2C), and the interaction of the stimulus frequency with the relative refractory period of the spiral ganglion cells (Wilson et al., 1997; Young, & Glynn, 1989).

Using Advanced Cochlear Implants to Identify the Phase-Locked Pitch Decoder

When the phase-locked pitch paradox was first identified in cochlear implant recipients, the technology was too primitive to provide fine enough control over temporospatial patterns of neural activity to be able to distinguish among possible pitch-decoding algorithms. Modern cochlear implants now have electrode contacts spaced approximately by a critical band and they permit very precise timing of

independently controlled stimulus waveforms on multiple, adjacent contacts. For example, the CLARION CII provides 1 μ sec resolution for arbitrary waveforms including biphasic pulse rates >100 kpps (Hartley, Kruger, Segel, & Faltys, 2003; Litvak, Overstreet, & Mishra, Reference Note 19). The effects of current spread and cross-talk between adjacent contacts, however, make it impossible to recreate directly the local temporospatial details of natural phase-locking to the acoustic traveling wave. Nevertheless, it should be possible to design electrical stimulation patterns that have noticeable and consistent effects on the perception of pitch and/or timbre. Systematic psychophysical studies of these effects might then be used to identify at least the broad outlines of the decoding algorithm used by the brain. That, in turn, might lead to the systematic design and selection of speech processing and stimulation strategies that reduce the perceptual dissonance that may be confusing many cochlear implant recipients.

High frequency pulsatile stimulation provides a unique opportunity to separate the effects of place and phase-locked gradients (Fig. 3), but first it is necessary to consider the nonintuitive biophysics of such stimulation. Symmetrical biphasic pulses were originally suggested for CIS because theoretically they should produce no residual membrane depolarizations in neurons that have not reached threshold for action potential initiation. In fact, it has long been recognized that membrane channels produce some rectification at subthreshold potentials, resulting in modest, residual polarization that contributes to undesirable crosstalk among adjacent sites of cochlear stimulation. The effects of residual depolarization and summation have been observed as relatively weak cross-talk between nearby electrodes even with relatively long duration biphasic pulses (80 μ sec/phase) at low frequencies (250 pps) for interleaving delays up to 640 μ sec (Bierer, & Middlebrooks, 2004). The solution to this is asymmetrical triphasic waveforms, which can be tuned to cancel these residual effects and reduce crosstalk (Eddington, Reference Note 9).

To achieve very high pulse rates, it is necessary to use very brief pulse widths. Under these conditions, the residual depolarization produced by biphasic pulses becomes the dominant mode of stimulation. The same biophysical theory that suggested the use of balanced biphasic stimulation (e.g., CIS strategy) predicts that threshold currents for such narrow pulses should rise at least to preserve constant charge (and even more steeply to compensate for the activation time of voltage-dependent sodium channels; Crago et al., 1974). If there were no residual depolarization of subthreshold neurons, then de-

creases in interpulse interval beyond the absolute refractory period (1 msec) should have little or no effect on neural recruitment. In fact, the thresholds for trains of narrow biphasic pulses continue to decline with pulse rate over the entire range from 200 to at least 6000 pps (Kreft, Donaldson and Nelson, 2004). That is because the effective stimulus is the nonzero net transmembrane current from each extracellular biphasic pulse, which is the equivalent of intracellular monophasic current pulses. Interpulse intervals of less than 1ms presumably permit integration of these monophasic current pulses by the spiral ganglion cells, which have time constants in this range (Loeb, White, & Jenkins, 1983). This suggests that the low thresholds obtained at high repetition rates are likely to be accompanied by a substantial increase in cross-talk among nearby channels (thereby defeating the original reason for changing from analog stimulus waveforms to CIS strategies).

Once the frequency of biphasic stimulation becomes high enough (>5 kpps), the spiral ganglion cells will no longer phase-lock to the individual pulses but will phase-lock instead to modulations of this carrier. At the onset of the carrier, this should result in phase gradients similar to those that would be produced by integration during the first phase of an infinitely long duration pulse; i.e., the neurons closest to the stimulation site would fire earlier in the high frequency train than those further away, which would need to integrate more of the weaker residual depolarization effects that they receive. Note, however, that this phasing would rapidly randomize in the case of a continuous high frequency train of narrow pulses. Such pulses provide the equivalent of a continuous depolarizing current, which would cause each neuron independently to integrate, fire and reset asynchronously (Fig. 3A). Thus the pitch associated with such a train will be dominated by the place pitch alone, with no conflicting information from rate or phase-locked pitch cues. Repetitive bursts of high frequency pulses (Fig. 3, B and C) will allow phase-locking to recur at the start of each burst if the pauses between them are long enough for a substantial decay of membrane depolarization. The shape of the phase gradients will then depend on the duration of the bursts and the intensity of the stimulation, just as it does for the longer biphasic pulses of the CIS strategy (Fig. 2).

If the repetition rate of bursts of high frequency pulses is high enough to eliminate any rate-pitch cues (>500 to 1000 Hz, depending on subject), then any pitch difference between the carrier bursts and the continuous carrier can be attributed to the phase-locked pitch decoder. A phase gradient with a

high acceleration (such as produced by including only one pulse per burst; see Fig. 3C, similar to Fig. 2A) would be closest to the condition for acoustical stimuli at the characteristic frequency of the place (e.g., Fig. 1A), so this stimulus should provide a strong reinforcement of the place pitch and it should sound the most like a pure tone when compared to the continuous carrier. A phase gradient with less acceleration (e.g., Fig. 3B) would normally be associated with a traveling wave tuned somewhat more apically (e.g., Fig. 1, B and C), so it should be perceived at a lower pitch (up to 1 to 2 semitones) and perhaps less tone-like than percepts produced by more conventional biphasic pulse trains at frequencies <1 kpps. A phase gradient that is too flat would tend to be ignored because it would normally be associated with a characteristic frequency at an apical place beyond a critical band away (e.g., Fig. 1D). Note that the random-phase condition in Figure 3A is very different from a coherent phase with a flat gradient such as Figure 2D, but it might be interpreted similarly by the local neural decoder. However, the only way to produce the flat gradient at one place is to stimulate at high intensity, which inevitably produces a spread of excitation in both directions plus a steep phase gradient at the fringes. It should be noted that the specifics of these predictions rest on assumptions about the nature of the phase-gradient decoder that are speculative. They are provided as examples of the rich set of experiments that can now be designed and performed to elucidate the nature of the decoder.

Another methodological tool could be built on the virtual channel strategy, which allows the place-pitch centroid to be steered continuously between the available electrode contact positions. This has been done successfully by stimulating two adjacent electrodes so as to create a peak of current density that lies between the two sites (Litvak, Overstreet & Mishra, Reference Note 19; McDermott, & McKay, 1994; Townshend, Cotter, Vancompernelle, & White, 1987; Wilson, Lawson, Zerbi, & Finley, Reference Note 31). It has also been possible to create virtual channels located outside the interval defined by the electrode positions by applying antiphase stimulation currents, effectively summing the cathodal phase of one stimulation site with the virtual cathode that tends to be created at a distance from the anodal phase of the other site. As with any electrical stimulation, paired stimuli seem likely to create orderly gradients of action potential initiation whose spatial slope should depend on stimulus pulse duration and intensity (indicated speculatively in Fig. 2D). The shape of these gradients could be further influenced by introducing small phase delays or shape differences between the two stimuli,

an experiment that has yet to be performed systematically. The CLARION CII architecture includes multiple stimulus channels that can apply independently controlled stimulus currents simultaneously to multiple electrode contacts (Hartley et al., Reference Note 15; Loeb, Faltys, & Voelkel, Reference Note 20). Its 1- μ sec temporal resolution is much faster than the likely sensitivity of the neural decoder for phase-locked pitch, which is estimated to be approximately 20 μ sec (Loeb, White, & Merzenich, 1983).

The actual temporospatial patterns of action potential generation will be difficult to predict for a particular stimulation train in a given cochlear implant recipient. They arise from the nonintuitive interaction of many different stimulation parameters and the heterogeneity of the spiral ganglion cells themselves, which differ in caliber and mediolateral position in the ganglion as well as pathophysiology (Young, & Glynn, 1989). Indeed, it is possible that such heterogeneity (or lack of it) is one of the most important factors that determines whether a subject is confused by strong gradients in phase-locking when using low frequency pulsatile strategies. That is, subjects with heterogeneously damaged spiral ganglion cells may have less difficulty with perceptual dissonance and less ability to perceive the effects predicted for the hypothetical experiments described above.

One important and generally overlooked factor is the shape of the potential gradient created across the spiral ganglion, which may account for unexpected results reported for monopolar versus bipolar channels (Drennan, Pflugst, & Xu, Reference Note 8) and single contacts versus virtual channels (Busby, Plant, Whitford, & Cowan, Reference Note 4). Fortunately, accurate models of the spread of stimulation current (Vanpoucke, Verbist, Briaire, Frijns, & Peeters, Reference Note 30; Zarowski, Vanpoucke, & Peeters, Reference Note 34) and the initiation of action potentials in spiral ganglion cells (Frijns, de Snoo, & Schoonhoven, 1995; Rubinstein, Miller, Mino, & Abbas, 2001) are now available. These can be used to identify sets of stimulation patterns that are most likely to produce perceptually compelling effects on the phase-locked pitch decoder. Such patterns can then be administered to cochlear implant patients, using conventional psychophysical testing plus careful assessment of subjective percepts to identify effects on perceived pitch and timbre.

Implications for Cochlear Implant Development

It remains to be determined whether cochlear implants can be improved by providing more appropriate cues to the actual neural decoder of phase-

locked pitch. A more immediately promising tactic may be to weaken the dissonant cues so that they are more easily ignored. This may be the net effect of the recent emphasis on pulse repetition rates that are much higher (>2 kpps) than necessary to avoid spurious rate-pitch sensations (including those that arise from beating of stimulus rates against refractory period; Wilson et al., 1997). In at least some patients, these benefits appear to outweigh the likely increase in cross-talk (in comparison to the longer duration biphasic pulses that are possible with lower repetition rates and that should produce relatively less rectification and less cross-talk). The beneficial effects of randomization of phase will be difficult to disentangle, however, from other putative benefits of very high frequency stimulus content (see Appendix below on Effects of Noise and Stochastic Resonance).

Postlinguistically deafened recipients of a cochlear implant often find it difficult to provide consistent pitch rankings among electrodes, at least initially. Novel stimulation patterns can result in unexpected and distracting senses of pitch that are not predicted from either the place or rate pitch cues inherent in the electrical stimulation parameters (Busby et al., Reference Note 4). This is not surprising if the electrical stimulation results in conflicts among pitch cues that have never before been experienced. If a group of such patients had somewhat different strategies for resolving conflicting cues before they lost their acoustic hearing, then it is not surprising that they differ greatly in the magnitude and nature of the perceptual dissonance that they experience and the speed with which they learn to resolve this dissonance into consistent pitch and speech percepts. Training systems for speech perception may be useful for poor users of cochlear implants (e.g., Fu, & Galvin, 2003; Fu, Galvin, Wang, & Nogaki, Reference Note 13), particularly if they are designed to deal with such perceptual dissonance by encouraging subjects to focus on the useful cues and ignore the erroneous ones.

Attempts to relate cochlear implant performance to objective electrophysiological and psychophysical test data have been discouraging (Blamey et al., 1996). Newer and more sophisticated tests have shown promise, but only in very small populations so far (Wilson et al., 2003). It will be particularly instructive if individual subjects respond distinctively to attempts to control neural phasing electrically, particularly if these responses correlate with their preferences for or performance with different speech processing strategies. Such information could provide the beginnings of a systematic approach to developing and selecting optimal speech

processing strategies for individual patients and/or training patients to overcome learned handicaps.

APPENDICES REGARDING RELATED PHENOMENA

I. The Problem of Timbre

Timbre is often defined as what is left over after pitch, loudness, and timing have been extracted (e.g., ANSI S3.20-1973). Many spectral and temporal cues probably contribute to sound qualities associated with timbre, a multidimensional attribute (Bismarck, 2004). At least some of what is called timbre may be related to the ways in which the three different neural mechanisms for encoding and decoding pitch interact. Multiple tones whose tonotopic representations are spaced at or less than a critical band give rise to strong percepts of dissonance and timbre (Plomp, & Levelt, 1965). It is likely that they also produce conflicting cues from the three pitch mechanisms. Closely spaced tones give rise to extraneous rate pitch cues from beating of their individual frequencies and they produce nonlinear interactive distortions of basilar membrane motion and unevenly distributed phase-locking of auditory neurons. During the development of acoustic hearing, the auditory nervous system has many opportunities to learn to resolve these discrepancies and to extract unified pitch percepts that correspond to the "true" fundamental frequency of naturally occurring sound sources, most of which produce harmonically related spectral peaks over much of the acoustic spectrum. Interestingly, individuals with normal audiograms differ substantially in their ability to discern pitch when artificial sounds are created with deliberately ambiguous cues (e.g., Houtsma, & Goldstein, 1972). This suggests that different individuals may learn to trust different cues in a given circumstance, perhaps akin to their ability to learn which cues are most reliable in the body motion task described earlier. But the pitch perception task is not quite a winner-take-all judgment because the residual discrepancies are not suppressed. Instead they may give rise to a perception of pitch complexity or ambiguity and they almost invariably contribute to the orthogonal percept of timbre.

II. Effects of Noise and Stochastic Resonance

The original justification for using very high frequency pulse trains in cochlear implant patients was to minimize the generation of spurious rate-pitch cues resulting from beating of acoustic signals against fixed-frequency pulse trains and the refrac-

tory periods of spiral ganglion cells (Wilson et al., 1997). Randomization of interpulse intervals (Chatterjee, & Robert, 2001) and amplitudes (Chatterjee, & Robert, 2004) and the addition of subthreshold current noise all represent more general strategies to optimize information transfer in a system that contains threshold nonlinearities (e.g., Maltan, & Harrison, 2002; Rubinstein, Wilson, Finley, & Abbas, 1999; Chatterjee, Robert, & Oba, Reference Note 6). Such strategies for cochlear implants were, in fact, suggested by the functionality of the intact nervous system in various nonauditory modalities (Morse, & Evans, 1996).

The specific application of the theory of stochastic resonance to the auditory system depends on assumptions that may not be valid. The current information theory models make the same assumption that underlies the design of cochlear implants, namely, that only place pitch matters (Morse, & Evans, 1996). To the extent that this is true, then stochastic resonance may contribute usefully to aspects such as dynamic range (Hong, & Rubinstein, 2003; Hong, Rubinstein, Wehner, & Horn, 2003). All of the strategies for exploiting stochastic resonance, however, are likely to have substantial effects on other pitch decoding mechanisms in the brain (e.g., Rubinstein, Hong, & Meyer, Reference Note 24), especially including phase-locked pitch (as noted above for high frequency pulses). If one of the limiting factors in cochlear implant performance is the subject-specific perceptual dissonance that arises from these other pitch decoding mechanisms, then it is not surprising that strategies based on stochastic resonance appear to encounter the same variability that has plagued the developers of "conventional" speech processing strategies (Büchner, Frohne, Battmer, & Lenarz, Reference Note 3). Furthermore, any improvement might be attributable to disrupting the coherence of erroneous cues (e.g., randomization of phase, as in Fig. 3A) rather than enhancing the representation of relevant cues, returning us full circle to the original justification for high pulse rates noted above.

III. Binaural Interactions

The temporal cues required to extract phase-locked pitch by any neural mechanism are probably of the order of 20 to 200 μ sec. The only mammalian neural processor known to operate with such sensitivity is that used to localize sound on the basis of interaural delay (ITD), which is thought to reside in the medial superior olive (MSO; Yin, & Chan, 1990). Synaptic transmission tends rapidly to degrade phase-locking, further implicating the MSO, the first brain stem nucleus in which information con-

verges from the two cochleas. The decoding mechanism can be characterized as a form of high resolution cross-correlation between signals originating from corresponding portions of the basilar membrane in each cochlea.

Teleologically, the next most salient feature of a sound after simple detection is perhaps the relative location of its source. It is possible that the highly specialized neural circuitry required to analyze interaural temporal delays evolved before and would have been available for later, sophisticated spectral analysis of sounds. Thus, it was natural to suggest that the MSO might also extract phase-locked pitch by cross-correlating signals arising up to a critical band apart from each cochlea (Loeb, White, & Merzenich, 1983). The resulting four-way cross-correlation has the interesting result of producing a two-dimensional representation of sound in which one axis represents phase-locked pitch while the second maps the angle of azimuth of the source of that pitch. Such a mechanism could contribute to the ability of normal hearing subjects to separate and attend selectively to multiple speakers even when their words overlap in spectral content, the so-called "cocktail party effect." Subsequent research on spatial cues for segregation of complex speech sounds suggests, however, that coherence of the harmonic structure and interaural loudness differences provide stronger cues than simple mapping of the spectra according to interaural time delay (Darwin, & Hukin, 1999).

The best cochlear implant recipients appear to decode interaural time-delays for electrical stimulation that are short enough ($<100 \mu\text{sec}$; Smith, & Delgutte, Reference Note 26) to suggest that they are using a specialized binaural pathway such as the MSO, although normal hearing individuals have even lower thresholds for acoustic clicks ($20 \mu\text{sec}$; Yost, Green, & Wightman 1971). If at least some of these patients are using the MSO to attempt to decode pitch information from the phase gradients induced by electrical stimulation, how might such decoding account for recent results from bilateral cochlear implants?

It has been reported that the loudness maps for each ear of a bilateral cochlear implant recipient must be fine-tuned in complex ways to achieve optimal performance when both implants are used together (Battmer et al., Reference Note 1), consistent with the notion that they are sharing common central circuitry such as the MSO. Commercially available cochlear implants do not permit bilateral synchronization with sufficient fidelity to influence systematically the high resolution cross-correlator hypothesized above. When more precise synchronization is applied using research equipment, most

cochlear implant subjects perform an order-of-magnitude worse than normal hearing subjects in detecting ITDs (Long, Eddington, Colburn, & Rabinowitz, 2003, but see Smith, & Delgutte, Reference Note 26). This may be a particularly sensitive indicator of heterogeneity among the surviving ganglion cells, which might be expected to degrade the phase coherence detected by the MSO. If so, then only some subjects are likely to benefit significantly from precise synchronization of bilateral cochlear implants.

Bilateral cochlear implant recipients experience widely varying benefits, which generally emerge only after many months of daily use (Litovsky, Arcaroli, & Parkinson, Reference Note 18; Ramsden, & Greenham, Reference Note 22), even if they are already well practiced in the use of one cochlear implant. This is reminiscent of the early days of multichannel cochlear implants, when it took months to years for most patients to adjust to the distorted dynamics and inconsistent fitting procedures of the primitive technology (Dorman, Dankowski, Mccandless, Parkin, & Smith, 1990). Most high performers now achieve most of their functionality almost immediately after fitting a unilateral cochlear implant; a subset of those who perform poorly initially improve gradually over time whereas a persistent minority remain chronically poor performers (Loeb, & Kessler, 1995; Wilson, 2000). One source of such heterogeneity may be insertion depth of the electrode and ability to learn to adjust to shifted and distorted frequency maps in the cochlea (Dorman, Loizou, & Rainey, 1997; Rosen, & Faulkner, Reference Note 23; Svirsky, Teoh, Neuberger, Silveira, & Suarez, Reference Note 28). As noted above, postlinguistically deafened cochlear implant patients may also be inherently heterogeneous in their learned neural strategies for acoustic speech perception. If they are lucky, the audiologist fitting their speech processing strategy can find one that produces conflicting pitch cues that are more easily ignored by their nervous system. If they are not so lucky, then they must attempt to relearn speech recognition based on unfamiliar cues, with more or less success. It is likely that all current implementations of bilateral cochlear implants are distorting important cues in ways that patients must learn to overcome. It remains to be seen if bilateral speech processing strategies (e.g., improved synchronization between corresponding cochlear places in the two ears) can be devised that immediately improve performance in at least some recipients.

Carlyon and Deeks (2002) reported an interesting paradox in the extraction of the missing fundamental (F0) from unresolved harmonic series presented

to normal hearing subjects. This ability generally deteriorates at $F_0 > 300$ Hz, similarly to loss of rate pitch in cochlear implant patients. The introduction of a contralateral acoustic reference signal produced a substantial improvement, depending on the frequency band of the harmonic series. This is consistent with the notion that at least some pitch perception mechanisms can integrate temporal information from both ears.

IV. Acoustic Simulations of Cochlear Stimulation

Cochlear implant researchers have long been frustrated by not knowing what cochlear stimulation actually “sounds like.” Acoustic simulations based on amplitude-modulated narrow-band noise sources appear to account surprisingly well for the effects of channel number and place, at least in the best cochlear implant recipients (Friesen, Shannon, Baskent, & Wang, 2001), but it is not clear how far the verisimilitude extends. These simulations are based on a pure place-pitch hypothesis of cochlear implant function. As we have seen above, however, the phase-locked neural activity inherent in electrical stimulation may modulate the center frequency and/or the bandwidth of the actual percepts.

More recently, researchers have attempted to extend these simulations to account for the “fine structure” that they anticipate will be evoked across the population of auditory neurons in response to electrical stimulation (e.g., Rubinstein et al., 2003; Nie et al., Reference Note 21; Stickney, Nie, & Zeng, Reference Note 27). It seems possible, however, that the simplifications and uncertainties buried in the underlying assumptions invalidate such extensions. First, selecting any particular aspect of fine structure depends on an implicit hypothesis about how that aspect is both encoded and decoded by the nervous system. Second, the relevant fine-structure that is actually created as a result of electrical stimulation may not be represented accurately (or at all) in the acoustic simulations. Third, failure to understand how the fine structure is normally decoded during acoustic hearing may result in hearing subjects being able to extract information from the simulations that they are not intended to hear (e.g., Nie et al., Reference Note 21).

Rather than using acoustic simulations to evaluate more complex speech processors, they might be used to represent more accurately the shortcomings of current speech processors and stimulation paradigms. The analysis above suggests that poor control of phase-locked pitch cues should produce random fluctuations of 1 to 2 semitones in the apparent pitch associated with each electrode place. Such fluctua-

tions could be introduced into the band-filters used to generate the acoustic simulations of cochlear implants. If some but not all normal hearing subjects experience substantial interference with speech perception, this would provide support for the notion that variability of preference and performance of postlinguistically deafened patients with cochlear implants is a product of learned cognitive strategies that predate the onset of deafness. Speakers of tonal languages such as Chinese appear to place relatively more importance on “fine structure” cues such as these pitch fluctuations (Xu et al., Reference Note 33), reinforcing the suggestion that their effects may be both learned and variable among postlinguistically deafened recipients of cochlear implants.

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