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Chapter 17
The Cognitive Auditory System: The Role of Learning in Shaping the Biology of the Auditory System

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17.1 Introduction

Since the 1980s, we have known that training will prompt a given cell in auditory cortex (AC) to alter its firing properties in response to a stimulus following training. My doctoral dissertation was among the first to demonstrate this (Kraus & Disterhoft, 1982). In the years since, we have learned a great deal about the role of the types of training, the strategies used to achieve learning, and trainee motivation on AC response plasticity. Except in rare circumstances, single-unit methodologies are unavailable to researchers interested in determining the effects of learning and experience on the human auditory system. Noninvasive electrophysiology, in the form of cortical evoked potentials (EPs), has served as an informative surrogate. Moving to suprathreshold stimulation and far-field recording methodologies, widely studied cortical responses such as the N1, mismatch negativity, P300 and "processing negativity" are valuable in characterizing neural plasticity in groups. However, they suffer from response variability, rendering them unsatisfactory as gauges of training-related plasticity *in individuals*. In addition, their slow voltage fluctuations, occurring hundreds of milliseconds after the evoking sound, offer poor renderings of the acoustics of the stimulus. Recently, there has been a resurgence of brain stem EP work. The auditory brain stem response to complex stimuli (cABR), coupled with advanced analysis methodologies, is a faithful gauge of acoustic processing, yet also reveals an auditory processing that is profoundly affected by external factors such as communication skills and training. The brainstem is a hub of sensory, cognitive and reward influences. As such, cABRs complement animal work in understanding an integrated, cohesive auditory system and the central-to-peripheral circuits that make auditory learning possible. My own scientific career path has somewhat mimicked that of evolution in the field, first exploring cortical plasticity at the single-unit level in animals, and then shifting focus to cortical evoked responses in humans and experimental animals, and now, with my focus on cABR. However, each phase of my career—though the approach and the tools have changed—has focused on *the cognitive auditory system*. And so we, along with the field as a whole, are moving toward approaching the many components of the auditory system—periphery, central structures, nonauditory cortex—as an integrated hearing circuit.

17.2 Anatomy of the Cognitive Auditory System

Information flow in the auditory system depends on a network of peripheral, subcortical and cortical nuclei with vast interconnectivity (Hackett, 2011). Auditory information processing is affected by the extensive corticofugal system, which exerts "downward" influence on the "upstream" afferent processing chain (Suga, 2008). Within the auditory pathway, corticofugal connections exist between auditory cortex and thalamic, collicular and peripheral structures (Winer, 2006). In addition, nonauditory regions, including visual, somatosensory, limbic, and association areas, enervate auditory centers (Budinger et al., 2006). Memory, attention, experience, communication skills, and learning influence the activation of the auditory system

Fig. 17.1 Schematic illustration of ascending and descending connections in the auditory system. This cross-sectional view includes the cochleae, as well as auditory brain stem and thalamus. Descending connections between auditory cortex and these lower auditory areas have been long established and studied. The investigation of the functional and physiological consequences of the reciprocal connections between cognitive centers (e.g., those responsible for executive functions like attention and memory), reward (limbic) areas, and the auditory pathway is an emerging field. (Image by Libby Karlinger Escobedo)

(Halpern & Zatorre, 1999; Tzounopoulos & Kraus, 2009). The vast interconnectedness of the auditory system, with its links to cognitive and reward centers, is represented in Fig. 17.1.

17.3 Cognitively Mediated Physiological Changes—Receptive Fields of Cortex

We now know that the auditory cortex, along with other primary sensory neocortical regions, is "a structure holding a strategic position in the interaction between bottom-up processes (dominated by the sensory input) and top-down processes (dominated by the state of the subject, including its past history, future goals and expectations, and hence mediating the meaning of stimuli, as well as states and actions associated with perception of these stimuli)" (Deliano & Ohl, 2009). Indeed, auditory cortex plasticity, both in primary (A1) (Weinberger et al., 1984) and nonprimary (Kraus & Disterhoft, 1982) regions, has been known since the 1980s.

A common visualization technique used to investigate auditory neural plasticity, both in cortex and subcortical structures, is the spectrotemporal receptive field

(STRF). Like a spectrogram, it depicts frequency on the ordinate, time on the abscissa. The color axis represents neural firing—both excitatory and inhibitory—and thus a best frequency and corresponding time delay (relative to stimulus) can be ascertained for the unit(s) under test. Used as a portrayal of characteristic frequency (CF), it enables quick visualization of changes in tuning that occur following intervention, such as noise exposure, ototoxic drugs, training, activation of other brain regions, and so forth. The exact nature and extent of the training-induced change in STRF depends on a number of *nonauditory* factors, demonstrating the role of cognitive factors such as motivation and emotion on auditory processing.

17.3.1 Type or Difficulty of Task

The sharpening, shifting, or otherwise changing of receptive fields of cortex generally is a result of a need to accomplish a task. Training establishes that a particular tone, for example, signals that a task must be performed to receive a reward or avoid punishment. Cortical tuning to this now behaviorally relevant tone is expanded and/or sharpened to accomplish the task accurately. The patterns of plasticity depend on whether the task type is avoidance or approach. Specifically, when a given tone is associated with punishment, the STRF reveals an increase in responsivity at the tone frequency; when it signals a reward there is a decrease (David et al., 2012).

17.3.2 Strategy and Attention

The strategy used to learn when to respond and when not to respond influences the tuning of auditory cortex, as does the particular element of the stimulus that bears information relevant to the task. A water reward paradigm, in rats, was designed such that shortly after a tone stops, a flashing light signals that continued licking will result in punishment. Some rats adopt a strategy to stop licking as soon as the tone ceases while others wait until the flashing light before stopping. Rats in the latter group have larger cortical reorganization after training, even when motivation level is taken into account (Berlau & Weinberger, 2008). Also in rats, a design was employed in which a particular feature of the stimulus (either frequency or intensity) was the relevant aspect for the task. The same stimulus was found to have a different reorganization effect depending on which aspect was attended to (Polley et al., 2006). Thus the attention, strategy, and motivation of an animal are crucial elements of AC reorganization.

17.3.3 Neurotransmitters

The shaping of auditory cortex is driven by neuromodulators, in particular acetylcholine. The behavioral relevance of a stimulus activates the nucleus basalis (NB), a highly cholinergic region of forebrain. Pairing tones with NB stimulation engenders changes in primary AC tuning and nonprimary AC selectivity similar to those seen with conditioning. Other neuromodulators, including dopamine and serotonin, also modulate AC learning (reviewed in Thiel, 2007).

A hot question in the auditory learning literature is whether or not a change of tuning in auditory cortex can be construed as "information storage" and thus memory. The view that AC itself meets the criteria of being a site of memory, not merely a processor of signals that lead to memories in "higher" cortical regions is held by Weinberger (2004). He argues that attributes seen in AC, such as rapid learning, consolidation, and long-term maintenance of plasticity, constitute the ingredients necessary for it to be classified as a site for storage of stimulus features of behavioral significance. Others disagree, noting that over time, AC map reorganization often normalizes to a pre-trained state; yet, the learned behavior endures (Kilgard, 2012), indicating that AC itself is not exhibiting memory. Whether AC is a storage site for learned stimulus features, whether learning is expressed in a neural code different from map reorganization, or some combination of the two, as is my view, the cognitive nature of AC is clear.

17.4 Cognitively Mediated Physiological Changes—Subcortical Regions

Auditory subcortical regions, like those in other sensory modalities, serve, in part, to propagate neural impulses from the periphery—the cochlea—to auditory cortex. Indeed, like their sensory cortical counterparts, there was a time when subcortical structures were thought to be either simple relay stations or, at most, centers of binaural processing. However, we now know that their enervation is bidirectional (Winer, 2006) and, like AC, they have plastic response properties. Of particular relevance to this chapter are the properties of the inferior colliculus (IC) of midbrain. This auditory subcortical nucleus shares some functional characteristics with primary visual cortex (Nelken, 2008), and viewed in this light, its experience-dependent plasticity is not entirely surprising. For a review of corticofugal enervation and learning-associated plasticity of IC and other subcortical regions, see Suga (2012). Here, we will mention a few studies that illustrate the functional plasticity of IC.

17.4.1 Importance of Descending Fibers in Learning

In a study of sound localization training, it was found that ferrets with ablated corticocollicular projections maintain their ability to localize sound. However, when one of their ears is plugged, resulting in the need to adjust to the new spatial cues of an altered soundscape, localization performance suffered compared to controls with intact corticocollicular fibers (Bajo et al., 2010). *Thus, facilitation of learning* *appears to be a chief role of the auditory efferent system, with the implication that learning can bring about subcortical physiological changes* via *top-down mechanisms*.

17.4.2 Online Implicit Learning of Sound

Inferior colliculus neurons have characteristic rate-intensity functions. That is, a given neuron, in response to sounds of varying intensities, might show increased firing up to a particular maximum intensity above which firing rates saturate—defining the dynamic range of the neuron. The dynamic range is the range over which there is a change in firing rate with increased intensity of stimulation. Above the saturation level, there is no meaningful distinction in the response to two different intensities. However, this dynamic range can be shifted in real time if the sound input is manipulated. If noise stimuli of varying intensities are presented with statistical distributions peaking, first at 39 dB and then at 63 dB, the rate-intensity functions shift such that the saturation level is higher for the 63–dB-centered stimulus set (Dean et al., 2005). These changing set points enable a much wider dynamic range than would be possible if such online modification of neural properties did not take place. Another example of online changes in response properties occurring in IC was demonstrated using an oddball paradigm in which stimulus-specific adaptation was discovered; there was a rapid increase in IC spiking if a stimulus was presented in a novel context compared to when it was presented in a train of other like-stimuli (Malmierca et al., 2009). A human analogue of online alteration of response properties was demonstrated by the differences between subcortical responses to identical tonal stimuli depending on whether they were presented in a random sequence or as components of a pseudolanguage (Skoe et al., 2013a).

17.4.3 Attention

It is also possible to see IC changes in humans with imaging and electrophysiological techniques. Recent studies have demonstrated an alteration in IC activation depending on attentional demands put on the listener (Rinne et al., 2008; Hairston et al., 2013; Lehmann & Schönwiesner, 2014). This implicates cognitive top-down control of a subcortical auditory nucleus tied into cognitive demands (Raizada & Poldrack, 2007).

The studies reviewed above largely describe online changes, coincident with the behavior that is learned. Changes brought about over longer time scales via enriched or restricted environments and past training are even more striking and have been seen in auditory cortex and subcortical regions of experimental animals (Knudsen, 1999; Engineer et al., 2004; Yu et al., 2007) and humans (Skoe & Kraus, 2012; White-Schwoch et al., 2013).

17.5 Cognitive Auditory Processing: Application to Human Communication

The importance of cognitive influence on hearing has huge implications in the realm of “training to hear.” Communication skills, such as listening to conversations in background noise or parsing the sounds of language in order to learn to read are skills that can be trained via protocols that exercise attention and memory, not simply the acoustics of sound itself (Hornickel et al., 2012b). Even in the absence of explicit training, implicit learning in the form of music performance and bilingualism also affects communication skills. Bilinguals, for example, enjoy advantages in executive function over monolinguals (Carlson & Meltzoff, 2008). Likewise, musicians have superior listening in noise abilities, enhanced auditory attention, and better auditory memory skills than nonmusicians, and these skills are reflected in the auditory system’s response to sound (Kraus & Chandrasekaran, 2010; Kraus et al., 2012; Strait & Kraus, 2014). Notably, these skills, though in the auditory domain, are somewhat far afield from music. Many, in fact, are in the realm of speech, a generalization which is predicted by Patel’s OPERA (overlap, precision, emotion, repetition, attention) hypothesis (Patel, 2011). In the next section, we discuss a neural metric—cABR—that is accessible in humans and enables the exploration of such experiential and training effects on the functioning of the cognitive auditory system.

17.6 Accessing the Cognitive Auditory System in Humans—cABR

In the human auditory system, we must infer that auditory system anatomy and physiological mechanisms are, for the most part, similar to those verified by work in experimental animal models. However, neurophysiological and imaging techniques bring quite a bit to the table and are not limited to animal models. Investigations in musicians, for example, indicate that this specialized experience with sound impacts brain structure and function (Herholz & Zatorre, 2012). Likewise, cortical electrophysiology is malleable with short-term training (Kraus et al., 1995; van Wassenhove & Nagarajan, 2007). In addition, cortical responses in language impaired populations differ from controls (Kraus et al., 1996; Jentschke et al., 2008). The auditory brain stem is also modifiable by learning and experience and, in this section, we focus on recent work in our lab and others’ on the auditory brain stem response to complex sounds (cABR) illustrating this phenomenon.

The cABR is accessible noninvasively in humans, and unlike cortical evoked responses, cABR offers a greater applicability in individuals and a more direct relevance to the evoking stimulus. Like its counterparts, the click- and tone-evoked brain stem responses, cABR is a measure of synchronous subcortical neural activity. A composite response originating largely in IC, it represents not only a gauge of afferent sound processing, but also a snapshot of the influences engendered by the corticocollicular networks. As such, *we view cABR as a metric of the entire auditory system*; *that is*, *we are not interested in* "*brainstem responses*" *per se*, *but in a measure that is accessible in humans and serves as a window into the cognitive auditory system as a whole*. In this section we review the two chief attributes of cABR—stimulus fidelity and experience dependence. In Section 7, we present some data that demonstrate the effect of training and experience on its response properties.

17.6.1 Stimulus Fidelity

Electroencephalographic recordings of sensory function are among the best tools that we have at our disposal for investigating the processing of auditory input in a noninvasive way in humans. Familiar exogenous auditory cortical evoked responses (EPs) such as P1, N1, and P2 and endogenous responses such as mismatch negativity and P300 are revealing in their ability to signal sound propagation in auditory cortex and its processing as sensory memory traces are formed and violated. However, cortical electrical activity offers a limited denotation of the features of the evoking sound, bearing only an abstract representation of the stimulus. Occurring hundreds of milliseconds after sound onset, these slow-voltage fluctuations recorded at the scalp convey little information about the complexity (or lack thereof) of the signal that evoked them. This is largely due to the lowpass filter characteristic of the auditory pathway and the convergence and overlapping of many sources that culminate at the scalp electrode. In contrast, although subcortical activity is also recorded from scalp electrodes and is subject to overlapping sources, stimulus presentation practices, selective filtering, and signal processing techniques together can largely eliminate the contribution of peripheral (i.e., cochlear microphonic) and cortical activity (Chandrasekaran & Kraus, 2010), resulting in a "brain stem" response, largely originating in IC. It is useful to point out that the nuclei responsible for the response are of secondary importance. *Although cABR features* "*brain stem*" *prominently in its name*, *utility as a measure of global auditory system processing should override the fact that its generation is of subcortical origin. The entire auditory system*, *cochlear hair cells included*, *is continually shaped by non-peripheral influences. Consequently*, *I feel that a paradigm shift away from labels such as early versus late and cortical versus subcortical is warranted*. The importance of selective filtering is that the resulting neural activity bears a remarkable resemblance to the evoking sound and exhibits experience dependence in a way that is not possible with other techniques. The response adheres to the stimulus on multiple time scales and visualization domains (Kraus, 2011; Li & Jeng, 2011). To take speech as an example (Skoe & Kraus, 2010a), at the longest timeframes such as the sentence or word level, onsets, offsets, stops, and other perturbations in speech envelope are maintained in the time-domain response as discrete transients. At the syllable level, the fundamental frequency (F_0) of the vowel is represented via the frequency-following response (FFR) that phase locks to the periodicity (voicing) of the utterance. The fine structure of the syllable—for example, the overtones that distinguish vowels or the frequency glides that characterize consonant-vowel syllables—are represented in the frequency domain by the harmonic content and phase attributes of the response and in the time domain with submillisecond timing. This high degree of correspondence between stimulus and response enables familiar signal processing routines such as autocorrelation, Fourier analysis, phase analysis, spectrograms, and so forth, to be applied to the response as well as to the stimulus in order to visualize sound processing of the auditory brain stem (Fig. 17.2).

17.6.2 Experience Dependence

Despite this high level of adherence to stimulus features, the cABR does not a represent a brain stem that is a passive conveyance of information from lower to higher auditory regions. *Subtle variations in the timing and spectrum of the response demarcate differences in individuals' auditory processing abilities based on experience*. This dual nature of the response is extremely appealing to me. Like STRFs in the cortex, it is rigorously signals-based in its elicitation and analysis approaches. Yet, this neural activity tracks with real-world experience and human communication, enabling scientists to address complex and practical questions regarding human communication with iron-clad objectivity. cABR therefore very comfortably fits my translational-educational bent, permitting a marriage of basic science and social and clinical issues. In a series of investigations our team has undertaken in the past dozen years, utilizing a number of different stimuli, cABR has been shown to track with aging, reading ability, cognitive abilities, musical experience, and bilingualism. In addition, training studies have demonstrated its short-term and online plasticity.

17.7 cABR as a Metric of Auditory System Plasticity

In this section and in Section 8, we review some work demonstrating the cognitive auditory system—comprising auditory-based skills, the factors that influence them, and experiential factors—using cABR recordings in humans, in most cases to speech sounds, as our approach. The cABR response properties include encoding of (1) the fundamental frequency (F_0), (2) pitch tracking, (3) harmonics, (4) changing formant frequencies, (5) onsets, and (6) response consistency.

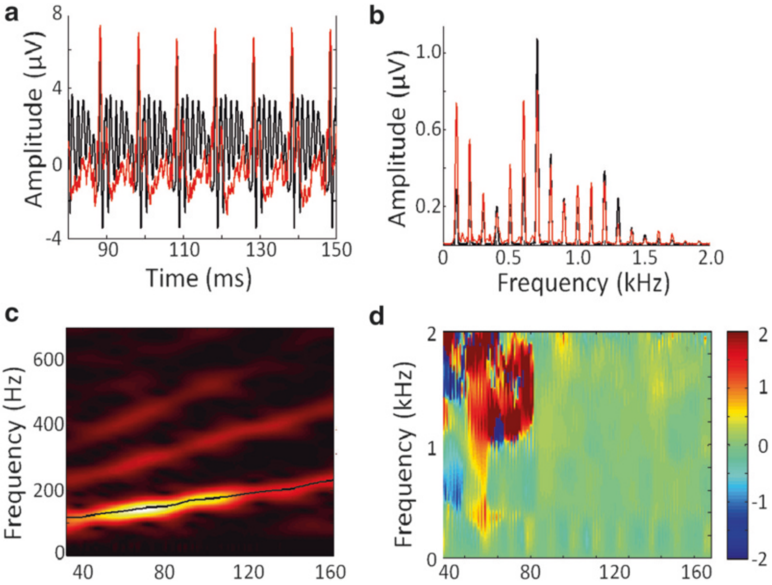

Fig. 17.2 cABR's adherence to the stimulus is demonstrated in these responses recorded from guinea pig scalp. (**a**) In the time domain, the response (red) closely follows the periodicity of this "a" syllable (black). The 70-ms portion of the stimulus waveform, which is arbitrarily scaled, has been time-shifted to visually align with the corresponding response peaks which actually occur about 9 ms later. (**b**) The same "a" syllable (black) closely matches the response (red) in the frequency domain. (**c**) Spectrogram of response to a "da" which has an upward sweeping fundamental frequency (F_0). The thin black line is an overlay of the F_0 of the stimulus. It is possible to derive an objective assessment of "pitch tracking" by comparing the frequency of the recorded F_0 to that of the stimulus over time. (**d**) A "cross phaseogram" comparing responses to "ba" and "ga." The colors depict timing differences, in radians, on a frequency-specific basis. The expected outcome, ga earlier than ba, is depicted with warm colors within the first 60 ms, corresponding to the consonant sounds. The large green field (~0 radians), from about 70 ms on, illustrates the similarity of the responses to the shared "a" sound

17.7.1 Encoding the Fundamental Frequency of a Signal

As shown in Fig. 17.2, the dominant feature in a harmonic-based signal like speech or music is the periodicity reflecting the dominant pitch. Even when the F_0 is absent, time-domain periodicity reveals the missing F_0. The F_0 in a cABR response can be viewed in either the frequency or time domain, and has been shown to be a predictor of the ability to hear speech in noise in children (Anderson et al., 2010b) and young and older adults (Anderson et al., 2011; Song et al., 2011; Anderson et al., 2012a), and in older adults it is a better predictor of hearing in noise ability than audiometric thresholds (Anderson et al., 2011). Phase locking to the F_0 also relates to the ability to selectively attend to an auditory signal amid distractors (Ruggles et al., 2011) and is better in bilinguals, and relates to their attention skills (Krizman et al., 2012). These skills use the F_0 to assist in the object grouping necessary to accomplish the task, and cABR demonstrates an objective basis of this grouping in humans.

17.7.2 Encoding the Changing F_0 of a Signal (Pitch Tracking)

Frequently, in natural stimuli, the F_0 of a signal is not flat. Questions, statements, emotional utterances, and other varieties of expression result in F_0 deviations that are perceived as pitch changes. Perception of a varying F_0 contour is especially important in tonal languages that use pitch to convey meaning. The cABR to the sweeping pitches found in Mandarin syllables has revealed differences in pitch processing between speakers of tonal versus nontonal languages. There have been demonstrations that, as with cortical EPs, the influence of language experience extends to the cABR. Specifically, to both Mandarin syllables and nonspeech analogs of Mandarin syllables (Krishnan & Gandour, 2009; Jeng et al., 2011), Mandarin speakers have more precise pitch tracking than English speakers; however, in infants born to tonal-language speaking families, this advantage is not seen at birth, confirming that the pitch-tracking advantage in tonal-language speakers is an experience-dependent effect (Jeng et al., 2011). This finding was extended in studies that saw an increase in cABR pitch tracking precision to Mandarin tones in musicians (Wong et al., 2007) and following linguistically relevant tone-syllable identification training in non-Mandarin speakers (Song et al., 2008; see also Carcagno & Plack, 2011). The cABR has also revealed group differences in F_0 encoding in children on the autism spectrum. A hallmark of autism is an inability to produce and detect prosodic elements in speech. In a study of autistic children, it was discovered that their tracking of pitch contours—a major contributor to prosody—in the brain stem was often less precise than in typically developing controls (Russo et al., 2008). Thus, the cognitive and affective meaning conveyed by F_0 fluctuations leaves its mark on brain stem processing of this sound property.

17.7.3 Encoding Speech Harmonics

Whereas the fundamental frequency can impart the percept of pitch to a speech signal, the arrangement of the harmonics is the primary information-bearing property in nontonal languages. The relative powers among the harmonics, determined by the filtering properties of the vocal tract, define the speech formants that differentiate vowels and contribute to consonant perception. Harmonics contribute to phonemic awareness and the mapping of sound to letters, which both underlie reading acquisition. Some studies from our lab support the link between speech harmonics and reading ability. Response power involving the higher harmonics of speech syllables is suppressed in cABRs of poor reading children relative to good readers (Banai et al., 2009; Hornickel et al., 2012a). The context of presentation of a longer syllable (repetitive presentation or embedded in a train of other syllables) affects the harmonic content of the response in normal readers, but the difference is suppressed in dyslexic children (Chandrasekaran et al., 2009). Indeed we have repeatedly observed cABR to relate most strongly to a complex cognitive skill such as reading rather than to basic psychophysical perception of sound properties (reviewed in Kraus & Chandrasekaran, 2010; Chandrasekaran & Kraus, 2012; Tierney & Kraus, 2013a).

17.7.3.1 Combination Tones

Nonlinearities of the auditory system also result in cABRs with spectral components not present in the evoking stimulus. Periodic activity at combination tone frequencies, that is, frequencies not present in the evoking signal, can arise in the response. The most straightforward example of this phenomenon is that demonstrated by responses to missing-F_0 stimuli (Galbraith, 1994). More complicated distortion products (e.g., cubic difference tones) also arise to two-tone interval stimulation (Krishnan, 1999), and experience with music impacts the salience with which they are represented in the cABR (Lee et al., 2009).

17.7.4 Encoding of Formant Frequency Timing

The relative timing of events in the formant transition, in stop consonants, enables the system to distinguish among them. We have studied cABR to consonant–vowel syllable pairs, for example, "ba" versus "ga." Poor reading is associated with poor phonological awareness, and this is reflected in ambiguity in cABR formant transition timing in contrastive consonants (Hornickel et al., 2009). Another related approach is the phase relationship between two responses. In the frequency domain, however, a cross-phase analysis presents a picture of the relative timing delays, such as how noise affects the entire response spectrum across time (Tierney et al., 2011). A particularly intriguing use of this cross-phase technique compares pairs of speech syllables. Stop consonant pairs, for example, t versus k or b versus g, are acoustically distinguished by differing formant trajectories. The differing formant frequencies of the syllables are represented by timing changes in far-field evoked responses and, in experimental animals, near-field responses from inferior colliculus corroborate the midbrain source (Warrier et al., 2011). The extent of the resulting inter-response phase difference shows a relationship with speech-in-noise perception ability and reading ability. People with the greatest phase differences in their responses have the best hearing in noise (Skoe et al., 2011) and in children the degree of phase difference is linked to pre-reading skills (White-Schwoch & Kraus, 2013). Musicians also have greater phase distinctions than nonmusicians (Parbery-Clark et al., 2012b). Although peak timing and phaseogram reflections of formant transition processing overlap, each also yields distinctive information (Tierney et al., 2011). By either measure—discrete timings or phase relationships—this neural reflection of critical speech–sound sensitivity represents a potent probe of a key feature of human communication.

17.7.5 Encoding the Onset of a Signal

Sound onsets, and also offsets and other transitions contributing to the envelope of a signal, evoke discrete neural events. The timings of these peaks, relative to the evoking event, are affected by nonperipheral factors. Examples of this include the ability to understand speech in noisy backgrounds (Anderson & Kraus, 2010; Hornickel et al., 2011), the aging auditory system (Anderson et al., 2012b), reading ability in children (Banai et al., 2009; Hornickel et al., 2009), and the context of the evoking sound with respect to its placement in a rhythmic musical background (Tierney 2013b). This latter finding has language implications given the importance of the processing of onsets in running speech. It should be stressed that response timing to a simple click-evoked stimulus generally does not depend on nonperipheral factors and click latencies always serve as important controls for all published cABR findings from our lab.

17.7.6 Response Consistency

Over the course of a cABR recording session, hundreds or thousands of repetitions of the signal are presented. The extent to which each evokes a similar response can be quantified via linear correlation. In practice, the signal-to-noise ratio of the response to any single stimulus event is too low to assess consistency. But, creating and correlating multiple partial averages can provide another means of assessing non-auditory influences on cABR. With techniques using first-half/last-half or odd/even pairs, response consistency was found to be lower in older adults (Anderson et al., 2012b), linguistically impoverished children (Skoe et al., 2013b), and poor readers (Hornickel & Kraus, 2013). This latter finding is consistent with increased neural variability in experimental-animal models of dyslexia (Centanni et al., 2013). Response consistency improves after auditory intervention (Hornickel et al., 2012b), is higher in bilinguals (Krizman et al, 2014) and is maintained in older adults who have musical training (Parbery-Clark et al., 2012a).

17.8 Cognitive Relationships with cABR

An observation, across studies of cABR, is that both overtly auditory skills such as the ability to hear speech in noise and general cognitive skills such as attention and memory relate to cABR metrics. An interesting pattern has emerged that the latter, more cognitive-centered skills, often show the stronger relationship to cABR. An example of this is demonstrated by the relationship of cABR to various measures of speech-in-noise perception. We use a variety of standardized measures of hearing in noise and there is a progression of strength of relationship of cABR F_0 encoding with the cognitive demand of the test (specifically, QuickSIN > HINT > Words in Noise). The general mechanism for this, we speculate, is that high-level processes such as working memory and attention are tapped in communication skills and learning, whether learning is defined as short-term, focused training, or lifelong experiential learning such as language or music. *It is the engagement of these cognitive mechanisms in the past that, in turn, shapes the nervous system's response to the acoustics of the signal in the present.*

Music, in fact, provides a superb model of the learning auditory system, in particular music training. As the OPERA hypothesis states, engaging in the study of music, for example, learning to play an instrument, is highly emotionally rewarding, relies on highly focused attention to precise acoustic sounds, and is highly repetitive, thus meeting major criteria of successful learning (Patel, 2011). With its honing of executive function and the overlap between music and language processing centers in the brain, music experience, even of limited duration (Skoe & Kraus, 2012; White-Schwoch et al., 2013), shapes communication skills as well as the nervous system's response to the acoustics of the speech signal (reviewed in Kraus & Chandrasekaran, 2010; Strait & Kraus, 2014; Kraus et al., 2012).

17.8.1 Neural Signatures of Cognitive Auditory Processing

Taken as a whole, from recent work from our lab and others, patterns have emerged associating subcomponents of cABR with communication skills, learning and experience. With cABR's capacity for application on the individual level, it is exciting to think about potential "neural signatures" that can inform the underlying mechanisms of sound-themed cognitive tasks. Toward that end, we have begun, with an admittedly limited scope, to organize some signatures that have emerged from some of the extant cABR findings. In Table 17.1, we have listed several broad categories corresponding to groups or communication activities in which we have seen particular cABR profiles.

- Successful *hearing in noise* is accomplished, in large part, by tracking the F_0 of the target speaker (Brokx & Nooteboom, 1982). Fittingly, there is a good correspondence between F_0 encoding in the brainstem and hearing in noise ability (Anderson et al., 2010b; Anderson et al., 2011, 2013; Song et al., 2011, 2012). Similarly, consonant–vowel formant transitions, as the fastest-moving and lowest-intensity components of speech, are most susceptible to noise (Nishi et al., 2010), and their representation in cABR timing aptly is associated with hearing in noise ability (Anderson et al., 2010a; Skoe et al., 2011).
- *Reading* ability, which has a strong relationship to phonological awareness (Ramus & Szenkovits, 2008) and is known to correlate with variable cognitive and sensory processing (Roach et al., 2004), aligns with processing of signal harmonics (Banai et al., 2009; Hornickel et al., 2012a), the acoustic differences between consonants (Hornickel et al., 2009; White-Schwoch & Kraus, 2013), and with response consistency (Hornickel & Kraus, 2013).
- In the *aging* system, there is a slowing of neural timing (Tremblay et al., 2002) and a decrease in inhibitory processes (Caspary et al., 2008), reflected by delayed response timing and inconsistent cABR. This is accompanied by reductions in harmonics, in response consistency, and in phase locking (Anderson et al., 2012b).
- A hallmark of *autism*, is difficulty with prosody; this is mirrored by diminished pitch tracking in the brain stem (Russo et al., 2008).

Table 17.1 Various forms of deprivation, decline and disorder (top rows) track with particular constellations of degradation in cABR measures. Experience and training (bottom rows), on the other hand, result in selective response enhancements. The cABR measures are described in Section 7

	Fundamental frequency	Pitch tracking	Harmonics	Onset timing	Formant frequency timing	Response consistency
Communication difficulty						
Hearing in noise	–				–	
Reading			–	–	–	–
Aging	–		–	–	–	–
Autism		–		–		
Linguistic impoverishment			–			–
Experience/intervention						
Musicianship	–	+	+	+	+	+
Bilingualism	+	+				+
Short term training	+	+			+	+
Online processing	+		+	+		

The bottom part of Table 17.1 lists five varieties of experience or training that impact cABR. The responses in the denoted categories are impacted by *musicianship* (Kraus & Chandrasekaran, 2010; Kraus et al., 2012; Tierney et al., 2013), *bilingualism* (Krizman et al., 2012, 2014), *linguistic impoverishment* due to poverty (Skoe et al., 2013b), *short-term training* in the form of computer-based training (Carcagno & Plack, 2011; Song et al., 2012; Anderson et al., 2013), and assistive listening devices (Hornickel et al., 2012b), or are influenced by mere *online exposure* to a stimulus (Skoe & Kraus, 2010b; Skoe et al., 2013a; Hairston et al., 2013). As can be seen by the wide variety of response property combinations, a mixing board is a better analogy for cABR than is a volume knob with respect to its ability to reflect communication ability and experience. When neural signatures of both categories of communication and experiential effects are better delineated, there exists a potential for practical remediation decisions. With more research, one might envision a cABR battery that, with the right mix of stimuli and analysis approaches, indicates, for example, an individual's difficulty in hearing in noise is best remedied by a particular intervention strategy.

17.9 Conclusions

In closing, we want to impress on readers that the auditory system can and must be viewed as a whole when any communication-related activity is to be considered. Auditory science is fractionized by disciplines—cognitive, peripheral, central. This is mirrored in the clinical realm, with discrete clinical practices targeting hearing, speech, and learning. Biology doesn't respect disciplines; and, happily, the field is moving toward a greater consideration of cross-disciplinary views. The brain works as an integrated unit, especially in learning, by which the auditory efferent system, in conjunction with nonclassical auditory brain regions, brings about fundamental changes in cortical and subcortical response properties within the classical auditory system. These cognitive mechanisms unleash the plastic properties that define and redefine “hearing” in behaving animals and human beings.

The auditory research field has been shaped, to a certain extent, by the available methodologies, especially as it pertains to human auditory function. Over the last several decades unit studies in animals, providing a cochleocentric focus on basic signal components and threshold tuning curves, have been joined by more corticocentric techniques such as functional magnetic resonance imaging (fMRI). There also has been a move toward utilizing signals at the suprathreshold levels at which we conduct the business of daily communication. The lens through which our lab and a growing number of worldwide colleagues view this cognitive auditory system happens to be the brain stem response. But the word “brain stem” must not be conflated with an outdated view of a handful of one-way signal-propagating nuclei. In fact, we have some regrets that the terminology “cABR” has caught on. Scientists using this technology—including ourselves—at times feel imprisoned by this nomenclature. Papers from my lab are guilty of propagating the problem, often including “brain stem” or “subcortical” in their titles. This automatically lessens their appeal to a segment of the scientific community concerned with auditory cortex or learning and plasticity and who equate ABR with “peripheral hearing test.” We are in fact, with cABR, studying cortical influences as much as local ones. What we must do, going forward, is to carefully present cABR as a way of examining how the auditory nervous system *in its entirety* processes fundamental components of sound, and how sound processing is modulated by online, short-term, and lifelong experience and developmental life stages. The auditory system, shaped by the activation of cognitive mechanisms, is a moving target and cABR moves right along with it. *An additional appealing aspect of this technology is its broad applicability*—the same exact stimuli, recording paradigms and analysis procedures can be used in humans from infancy to old age (Skoe et al., 2014), and in animal models (Warrier et al., 2011). Owing to cABR’s magnificent transparency to the evoking signal, its utility in individual humans, and its malleability in response properties, it provides an unprecedented snapshot of the inner workings of the vast, dynamic cognitive auditory system.

17.10 Future Directions

Although the plasticity of primary auditory pathway regions was confirmed 30 years ago, there is a continued hesitancy to pursue its applicability in research on learning and experience in humans. Brain stem- and early cortical-evoked EEG recordings are often dismissed as afferent-driven "obligatory" response to sound and the search for plastic response properties is largely constrained to responses such as early left anterior negativity, mismatch negativity, and others, which invoke associational processes such as sensory memory or linguistic knowledge. In the last decade, however, there has been a flurry of research in the malleability of responses formerly viewed as immutable. In particular, brain stem responses, which long have been seen as just the opposite, are proving to be an exciting window into the dynamicity of the auditory system. A huge advantage cABR has over many other evoked response measures is that it has a high level of reliability on an individual level and, in the absence of intervention, is stable and quite replicable. *As such, it has the potential to move outside the lab and into a role in the clinic, in schools, and in industry: venues where the impact of hearing on assessment and understanding of the biological bases of learning, training, and education is of vital interest*.

There are remaining questions about the manner by which auditory learning proceeds. Work remains to be done that combines cABR, cortical physiology, listening, and cognitive testing in a controlled longitudinal basis. In this way, developmental and learning-related time courses can be mapped with the goal of synthesizing the auditory cortical, subcortical, and cochlear findings into a cognitive auditory system model, each part of which is instrumental in learning and plasticity.

17.11 Summary

The auditory system comprises a vast network of interconnected peripheral, subcortical, and cortical centers. These circuits are bidirectional and extend beyond classically defined auditory pathway. Limbic and association areas have direct input to this auditory network, and there is clear evidence that cognitive processes such as attention, memory, emotion, and motivation impact the auditory processing of sound. This chapter reviews some of the anatomical and physiological underpinnings of these cognitive processes. Finally, it presents data demonstrating a means of physiologically accessing the cognitive auditory system in humans via cABR, and proffers its application in the assessment of and research into human auditory-based communications.

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