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## Auditory Division of the Statoacoustic Nerve

### ► Auditory Nerve

## Auditory Event-related Potentials

### ► Auditory Evoked Potentials

## Auditory Evoked Potentials

NINA KRAUS<sup>1</sup>, TRENT NICOL<sup>2</sup>

<sup>1</sup>Departments of Communication Sciences, Neurobiology and Physiology, Otolaryngology, Northwestern University, Evanston, IL, USA

<sup>2</sup>Department of Communication Sciences, Northwestern University, Evanston, IL, USA

### Synonyms

Auditory event-related potentials; ERP

### Definition

The firing of neurons results in small but measurable electrical potentials. The specific neural activity arising from acoustic stimulation, a pattern of voltage

fluctuations lasting about one half second, is an auditory evoked potential (AEP). With enough repetitions of an acoustic stimulus, signal averaging permits AEPs to emerge from the background spontaneous neural firing (and other non-neural interferences such as muscle activity and external electromagnetic generators), and they may be visualized in a time-voltage waveform. Depending upon the type and placement of the recording electrodes, the amount of amplification, the selected filters, and the post-stimulus timeframe, it is possible to detect neural activity arising from structures spanning the auditory nerve to the cortex.

### Characteristics

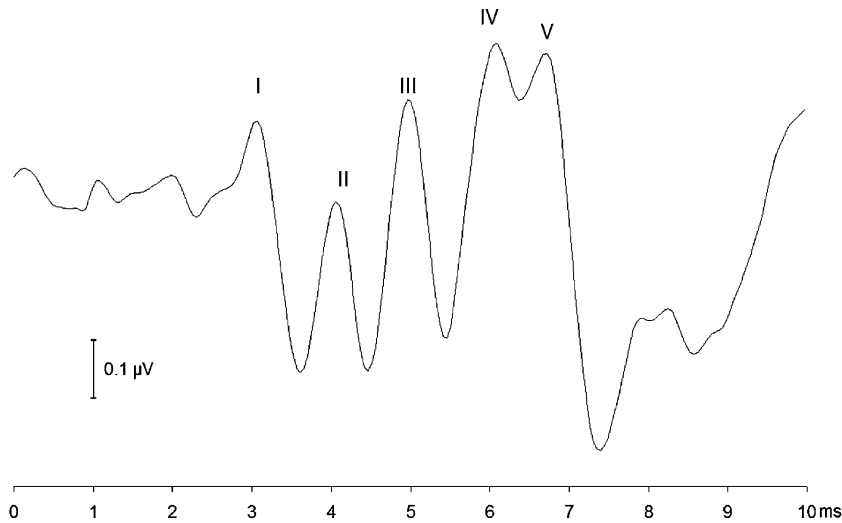
In general, as the time after stimulation (►latency) of a response increases, the neural generator becomes more central. In far field recordings from humans, the three typically used response classifications, based on response latency, are: early (the first 10 ms), middle (10–80 ms) and late (80 ms to 500+ ms). In terms of generators, these classes correspond roughly to brainstem, thalamus/cortex and cortex, respectively [1].

### Early Latency

Waves arising in the first ten ms after stimulation include both receptor potentials from the cochlea and neurogenic responses arising from the auditory nerve and low midbrain structures. With a near-field recording technique known as ►electrocochleography (►ECochG), two receptor potentials, originating in the cochlea's hair cells, can be recorded from the vicinity of the ear drum: the cochlear microphonic and the summing potential. They are AC and DC potentials, respectively, have an effective latency of zero, and last the duration of the stimulus. A millisecond and a half later, the dual-peaked neurogenic compound action potential of the distal auditory (eighth cranial) nerve can also be seen with ECochG. In contrast, using far-field electrodes, neurogenic responses known as the ►auditory brainstem response (ABR), can be recorded from the scalp (Fig. 1) [2].

These waves depend upon synchronous firing in the first relays of the afferent auditory pathway. For a given stimulus type (often an abrupt broadband click) and intensity level, the expected latency of ABR peaks falls within a very tight range (less than half a millisecond). Deviations from this range are useful in clinical diagnoses.

In particular, the ABR is a valuable objective measure of hearing. With decreasing stimulus intensity, wave latencies increase systematically until the hearing threshold is reached, below which the response is absent. Thus, an accurate measure of hearing threshold is possible in individuals who are unable to be tested behaviorally. Although there is a developmental time course (adult-like responses are attained by age two),



**Auditory Evoked Potentials. Figure 1** Early-latency auditory evoked potentials. The auditory brainstem response.

it is possible to test hearing in newborns with age-appropriate norms. Importantly, the ABR is unaffected by sleep or sedation, so obtaining hearing thresholds in babies or other uncooperative individuals is possible.

A second major clinical use of ABR is in the detection of lesions, tumors, demyelination, or conditions that cause increased intracerebral pressure (e.g., hydrocephalus, hematoma). ABR morphology, peak and interpeak latencies can have distinctive patterns that alert skilled clinicians to neural damage (e.g., eighth nerve tumors). Another major use of ABR is intraoperative monitoring. During neurosurgery, monitoring of ABR enables an immediate indication of whether any of the structures involved in the auditory pathway have been put at risk. Finally, the brainstem response provides a measure of neural synchrony necessary for normal perception of sound [3].

#### **Brainstem Responses to Complex and/or Long Stimuli**

Typical recordings employ short duration, relatively simple stimuli. However, complex sounds, some quite long in duration, are increasingly being used. Brainstem response to speech sounds can be used as a biological marker of deficient auditory processing associated with language and learning disorders [4]. A brainstem response whose nature depends on a long-duration stimulus is the ► **frequency-following response** (► **FFR**). The FFR, also known as auditory steady-state response, is an index of phase locking to a periodic stimulus. Examples of FFR-inducing stimuli are pure or modulated tones, tone complexes, modulated noise and speech [5]. Recorded from the scalp in humans, the FFR is a phase-locked response that, depending on electrode placement and stimulation and recording techniques, originates from as early in the auditory pathway as the auditory nerve or as late as the rostral brainstem. It is a measure of

both spectral and periodicity encoding, and because it is readily detectable in individuals, it has utility as a clinical measure of those processes as well as of hearing level. Brainstem responses are influenced by lifelong and short-term auditory experiences [6].

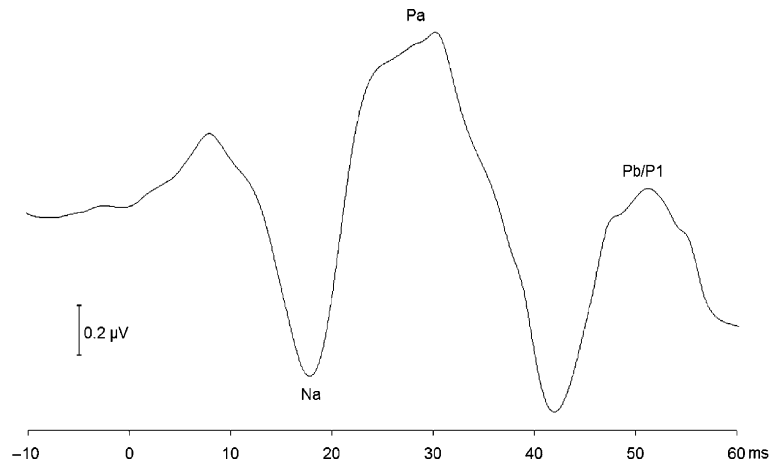
#### **Middle Latency**

The waves following the ABR, up to roughly 80 ms, are collectively known as the middle-latency response (MLR) (Fig. 2) [7].

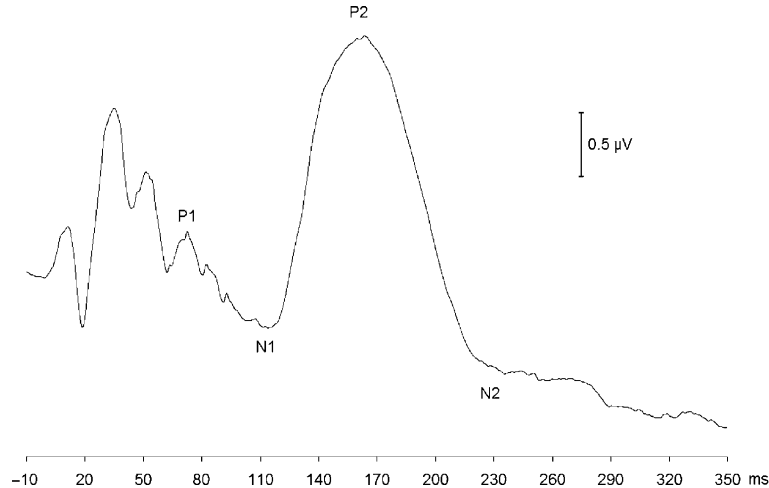
Although responses in this time frame are less mappable to specific neural generators than the earlier ABR waves, the thalamus (P0, Na) and cortex (Pa, Nb, P1) are involved. (Note: Unlike ABR waves, the names of middle- and late-latency responses typically begin with P or N indicating positive or negative polarity.) As ABR requires a high degree of neural synchrony, individuals with certain neurological disorders may exhibit absent ABRs despite normal hearing. Thus, MLR can be useful in assessing hearing sensitivity. For this same reason, a lack of sufficient synchrony in response to low frequency signals often makes MLR superior to ABR in assessing low-frequency hearing. Two major caveats in MLR as a hearing measure is that it does not reach its mature morphology until adolescence, and in children, there is a strong influence of sleep state.

#### **Late Latency**

Late-latency (>80 ms) AEPs, historically the first discovered, are cortical in origin and are much larger and lower in frequency than early and middle-latency potentials. Highly dependent upon stimulus type, recording location, recording technique, patient age and state, the late-latency responses may differ dramatically in morphology and timing and may overlap one another. Thus, categorization of responses



**Auditory Evoked Potentials. Figure 2** Middle-latency auditory evoked potentials.



**Auditory Evoked Potentials. Figure 3** Late-latency auditory evoked potentials. Exogenous responses.

into two broad types, exogenous and endogenous, is useful in describing these late potentials. Exogenous responses, which also describe early and middle-latency potentials, are more-or-less obligatory responses to a sound. Endogenous responses typically require a stimulus manipulation or the performance of a task by the patient.

#### **Exogenous Responses**

The archetypal late-latency exogenous responses are illustrated in Fig. 3.

Beginning with P1 (which is sometimes classified as middle-latency) at about 80 ms through to N2 at about 250 ms, all are cortical in origin and maximal in amplitude at the central top of the scalp. The maturational time course of the various components varies. Late cortical responses do not reach maturity until post-adolescence. They have value in assessing

cortical auditory processing. In addition to the classic pattern of responses to stimulus onset, changes within an ongoing stimulus also evoke a response called the acoustic change complex (ACC) [9]. Tones or tone complexes changing in frequency, complexity or intensity and speech syllables are typical stimuli. The response can be evoked by an acoustic change that is very near threshold.

Bridging the exogenous and endogenous categories is the **mismatch negativity (MMN)**. MMN is an acoustic change detector. It is evoked by a sequence of identical sounds that is interrupted occasionally by a different sound. This stimulus presentation technique is termed “oddball paradigm.” The response to that infrequent stimulus differs from that to the main stimulus, and appears as a slow negative deflection in the 150–300 ms time frame. The types of stimulus manipulations that evoke MMN include intensity,

frequency and complexity, and the contrasting stimuli can be at (or even below) perceptual threshold.

### Endogenous Responses

Endogenous (literally “born within”) potentials are those that, while induced by external stimuli, originate not as an obligatory consequence of the inducing sound, but rather due to some level of cognitive processing. Examples of endogenous AEPs are the P300 and N400. Sequentially occurring later in time, the P300 and N400 represent successively higher levels of sound processing. Evoked using the oddball paradigm, the classic P300, unlike MMN, only occurs when the listener is consciously attending to the stimulus aberration. P300, which is also evoked by other sensory modalities, is considered an index of cognition because stimulus evaluation and classification must take place [10]. The response is further divided into P3a and P3b components. P3a either appears to a distracter stimulus which is presented along with the targets and non-targets within the oddball presentation, or, if stimulus differences are large enough, with no task at all. This component has more frontal lobe contribution than the classically elicited parietal-centered P3b. A higher level of cognition is required for the N400 response [11]. It requires a speech stimulus, and occurs in response to semantic incongruity and thus is an indication of language processing.

### Considerations

A number of considerations and caveats are involved in the recording of reliable auditory evoked potentials. No response is monolithic, either in its etiology or in interpretation. A thorough description of stimulus factors alone could fill a volume: the length, intensity, complexity and repetition rate of the stimulus all affect the responses. Some responses differ dramatically depending upon whether the stimulus is delivered to one or both ears or whether there is accompanying visual stimulation; others are relatively unaltered by these factors. Characteristics of the recording device, particularly filters, also have an effect on response recording. Successively later responses have increasing low-frequency content and high-pass filters must correspondingly be opened. However, with increasingly more energy being passed on the low end, recordings are more prone to contamination by non-stimulus related activity: artifacts. Artifacts fall under two categories, those internal to and external to the testee. Internal artifacts include eye blinks, movements, muscle contractions including the involuntary sound-evoked postauricular muscle (PAM) reflex, and brain activity that is unrelated to the sound stimulus. External artifacts are those arising from electrical sources such as AC power line and the electrical signal traveling

through the earphone or loudspeaker cables (stimulus artifact). The degree to which artifacts adversely affect response recordings depends upon how alike in frequency the artifact and the response are. For example, eye blinks are very low in frequency, and thus are more damaging to low-frequency late-latency responses. Most artifacts are random in time of occurrence. Two exceptions are stimulus artifact and PAM. Stimulus artifact lasts as long as the stimulus. Therefore, it is not a concern if the stimulus is a 100  $\mu$ s click and the response of interest is the middle-latency Pa. However, the stimulus artifact from a 5 ms tone burst may obliterate an early-latency brainstem response. PAM reflex occurs in response to the stimulus in the 15 ms timeframe and thus most affects middle latency responses.

Much information can be gleaned from AEPs for both clinical and theoretical purposes. As the power and speed of computers increases, multiple-channel recordings and advanced signal processing techniques are better able to inform us about the underlying neural processes that are signified by these minute perturbations in the electroencephalographic activity resulting from auditory stimulation. Together with advances in neural imaging, the exquisite timing resolution of AEPs can help us approach a better understanding of the biological bases of auditory function responsible for human communication such as speech and music.

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## Auditory Maps

### ► Tonotopic Organization (Maps)

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## Auditory-Motor Interactions

WALTER METZNER  
UCLA Department of Physiological Science,  
Los Angeles, CA, USA

### Definition

Interactions between hearing and various motor functions, such as protective reflexes and vocal behavior.

### Characteristics

Auditory signals guide a multitude of behavioral responses from simple reflex motor patterns for orientation to complex vocal communication behaviors in virtually all vertebrates and insects. Hence, auditory stimulation can elicit anything from simple motor patterns, such as head/neck turns or ear movements, to complicated, highly coordinated interactions of several motor patterns, such as calling, breathing, and postural changes that occur, for example, during birdsong. In turn, certain motor patterns, especially those associated with vocal behavior, can also affect how the brain processes auditory signals.

### Auditory Orientation Reflexes

Orienting movements of the head, neck and/or eyes in response to auditory signals are generally thought to be controlled by auditory input to the superior colliculus in mammals, or its homologue structure in birds, the optic tectum. Most of our knowledge about what controls head movements in response to external signals is based upon studies of visually guided orienting responses, where the topographic representation of the stimulus that ultimately guides the motor response is naturally

determined by the retinotopic organization of the visual system. Auditory input to the superior colliculus/optic tectum is topographically organized only in barn owls. In mammals, the representation of auditory space appears to be less developed, and is often even more complicated by movements of the external ears, or pinnae. Very little is therefore known about the neuronal basis of acoustically elicited orienting responses. It appears that output from the superior colliculus/optic tectum to small areas in the midbrain tegmentum mediate the sensory-motor transformation of stimulus location into a direction-specific pre-motor command. This in turn gives rise to a directed behavioral response through activation of the various pools of motor neurons in the brainstem and spinal cord that control head/neck turns, turns of the body axis, and/or eye movements.

### *Pinna Movements in Mammals*

The mammalian pinna plays an important role in sound localization, especially for sources in the midsagittal plane, which generate minimal interaural disparities. In species with mobile external ears, the pinnae can be oriented independently of the head's position, thus aiding in sound localization by allowing the animal to obtain multiple samples of an acoustic object. In such mammals, auditory targets elicit stereotyped pinna movements that typically consist of two parts: a short-latency component that is time-locked to the onset of the sound and a second long-latency component that is highly correlated with eye movements and is probably part of the animal's general orientation behavior. The second, slower response most likely involves the superior colliculus, and might be mediated by pathways linking the superior colliculus with the facial nucleus, either via the reticular formation (tectoreticular–facial pathway) or via the paralemniscal area (tectoparalemniscal–facial pathway). In particular, the paralemniscal area, situated in the lateral midbrain tegmentum, supplies an elaborate network of monosynaptic excitatory and inhibitory inputs to the medial portion of the facial nucleus, where the motoneurons that innervate the muscles of the pinna are located. It is not clear, however, if the superior colliculus is also involved in mediating the initial, faster response. This component of auditory-evoked pinna movements might be driven directly via the paralemniscal area, which receives multiple, binaural inputs from the ascending auditory pathway, notably from the dorsal nucleus of the lateral lemniscus.

### Acoustic Startle Response

The startle response is a fast reflexive response to intense, unexpected acoustic, tactile or vestibular stimuli and protects the animal from injury by blows or predatory attacks. The acoustic startle response (ASR) of mammals, including humans, consists of a quick eyelid-closure and a contraction of facial, neck