The Role of Event-Related Brain Potentials in Assessing Central Auditory Processing

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Abstract

The perception of complex acoustic signals such as speech and music depends on the interaction between peripheral and central auditory processing. As information travels from the cochlea to primary and associative auditory cortices, the incoming sound is subjected to increasingly more detailed and refined analysis. These various levels of analyses are thought to include low-level automatic processes that detect, discriminate and group sounds that are similar in physical attributes such as frequency, intensity, and location as well as higher-level schema-driven processes that reflect listeners' experience and knowledge of the auditory environment. In this review, we describe studies that have used event-related brain potentials in investigating the processing of complex acoustic signals (e.g., speech, music). In particular, we examine the role of hearing loss on the neural representation of sound and how cognitive factors and learning can help compensate for perceptual difficulties. The notion of auditory scene analysis is used as a conceptual framework for interpreting and studying the perception of sound.

Key Words: Streaming, speech, ERP, attention, auditory, perception, hearing loss, auditory scene analysis

Sumario

La percepción de señales acústicas complejas, tales como el lenguaje y la música, dependen de la interacción entre el procesamiento auditivo central y periférico. Conforme la información viaja de la cóclea a la corteza auditiva primaria y de asociación, el sonido entrante se somete un análisis progresivamente más detallado y refinado. Se cree que estos varios niveles de análisis incluyen procesos automáticos de bajo nivel que detectan, discriminan y agrupan los sonidos que son similares en cuanto a los atributos físicos, como la frecuencia, la intensidad y la localización, así como procesos dirigidos por esquemas de más alto nivel, que reflejan la experiencia y el conocimiento del sujeto del ambiente auditivo. En esta revisión, describimos estudios que han utilizado potenciales cerebrales relacionados con el evento, para investigar el procesamiento de señales acústicas complejas (p.e., lenguaje, música). En particular, examinamos el papel de las pérdidas auditivas sobre la representación neural del sonido y de cómo los factores cognitivos y el aprendizaje pueden ayudar a compensar las dificultades perceptivas. La noción de un análisis de la escena auditiva se utiliza como un marco conceptual, para interpretar y estudiar la percepción del sonido.

Palabras Clave: integración, habla, ERP, atención, auditivo, percepción, pérdida auditiva, análisis de la escena auditiva

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Imagine this scenario. A businessman is sitting in a board meeting with several other colleagues. They are seated around a long oval table, looking in the direction of a projection screen. The group leader describes each unit of sale, spoken from the back of the room while year-end profit reports are projected on the screen. Not only do colleagues have their backs to the speaker, the room is darkened, so best to see the text and figures on the screen. The fan on the video-display system is noisy, as is the overhead ventilation system that pipes in chilled air. It is Friday, and people are restless, engaging in small talk, eager to start the weekend.

This type of listening environment is complex and common. The businessman complains that it is difficult for him to understand what is being said when there are too many noises around, and he is frustrated because he cannot hear the information he needs to do his job. So the businessman consults with an audiologist for assistance. The audiologist does what he or she is trained to do; he or she measures the individual's hearing thresholds to determine if there is hearing loss. Depending on the audiometric results, the audiologist might recommend a hearing aid (or assistive listening device). The businessman leaves the office hoping that his difficulties in following a conversation in noisy situations will be resolved. Unfortunately, rehabilitation is not that simple. Remediation not only requires that the speaker's voice be audible, the person needs to be able to separate sound sources that occur simultaneously and at the same time integrate information from the task-relevant message such that word and meaning can be extracted from the speech signals (i.e., auditory scene analysis). In addition, the person must be able to ignore competing signals and use contextual information to complement and integrate both auditory and visual information. Because hearing is dependent on sensory and cognitive processing, it is likely that sensory-neural hearing loss, dysfunctions in central auditory processing, and a struggle to selectively attend to a voice in the presence of competing noise all contribute to the businessman's problem.

At work or at social gatherings, many sounds occur at the same time and yet most listeners are adept at filtering and sorting the information that flows through their ears. Unfortunately, as was described in the earlier scenario, there are many instances in which the ability to hear is compromised either because of the presence of competing noise and/or because the listener has hearing loss. Hearing disorders may have several patho-physiologies including damage to the sensory system ("peripheral") and/or dysfunction within the neural pathways and auditory cortices ("central"). Although the most common intervention for peripheral hearing loss is to increase the audibility of sounds with the use of hearing aids, this approach improves the audibility of sound but it does not compensate for central auditory disturbances that may coexist with or arise from peripheral pathology. It is therefore not surprising to find people who report difficulty hearing, even after being fit with a hearing aid. Impaired speech understanding, especially in adverse listening situations, is likely related to changes in central mechanisms critical for the perceptual organization of the incoming acoustic information to form accurate representations of the various sound sources present in the environment, in addition to weak and distorted signals relayed from the ear. This is especially true for speech and music perception because the stimuli are highly complex and are dependent on various stages of analyses, including low-level automatic processes that detect, group and/or segregate sounds that are similar in physical attributes (such as frequency, intensity, and location); as well as higher-level schema-driven processes that reflect listeners' experience and knowledge of the auditory environment.

Auditory scene analysis is one framework to guide our research with respect to the putative mechanisms involved in auditory perception and cognition. This conceptual framework can be particularly useful for thinking about hearing impairment and the processing of complex acoustic environments because it acknowledges both that the physical world acts upon us as our perception is influenced by the physical structure of sound (i.e., bottom-up contributions), just as we are able to modulate how we process the incoming signals by

focusing attention on certain aspects of an auditory scene according to our goals (i.e., top-down contributions). As for bottom-up contributions, sounds emanating from the same physical object are likely to be acoustically similar; they might begin and end at the same time, share the same location, have similar intensity and fundamental frequency (f_0), and have smooth transitions. Consequently, it has been proposed that acoustic, like visual, information is perceptually grouped according to Gestalt principles of perceptual organization, such as grouping by similarity and good continuation (Bregman, 1990). Many of the auditory grouping processes are considered automatic or "primitive" since they are found in infants (McAdams and Bertoncini, 1997), as well as non-human species such as birds (Hulse et al., 1997; MacDougall-Shackleton et al., 1998), and monkeys (Izumi, 2002). With respect to top-down contributions, evidence shows that our knowledge from previous experiences with various listening situations influences how we process and interpret complex auditory scenes. For instance, the use of prior context during a speech identification task helps listeners to identify the final word of a sentence embedded in noise (Pichora-Fuller et al., 1995). Similarly, it is easier to identify a familiar melody interleaved with distracting sounds if the listener knows in advance which melody will be presented (Dowling et al., 1987), or if they have been presented with the same melody beforehand (Bey and McAdams, 2002). These effects of context are consistent with higher-level schema-driven processes involve the selection and comparison between current auditory stimulation and prototypical representations of sounds held in long-term memory.

The example of the businessman described earlier represents a real-world auditory scene analysis problem in which an individual is faced with the problem of parsing simultaneously active sound sources while at the same time trying to integrate and follow an ongoing conversation. Understanding how speech and other complex sounds are translated from the single pressure waves arriving at the ears to neural sound object representations is therefore an important process to consider. This knowledge can influence

the way we view auditory rehabilitation. It can help us understand why hearing aids might be insufficient for some people with hearing loss, and it can spawn new approaches to (re)habilitating people (Souza and Tremblay, 2006; Tremblay et al., 2006b).

In the last 10 years, there has been a great deal of research aimed at identifying the neural underpinning of central sound processing, using various approaches including single-cell recording in non-human primates, functional magnetic resonance imaging, and scalp recording of neuroelectric or neuromagnetic brain activity. A review of all neurophysiological and neuroimaging studies is beyond the scope of this article. For this reason, we focus our attention on a few studies that have utilized scalp recorded event-related potentials (ERPs) to assess sensory and cognitive aspects of central auditory processing.

EVENT-RELATED POTENTIALS

Scalp recorded human ERPs are a powerful technique for investigating the neural correlates of central auditory processing because they permit the opportunity to study the brain activity with exquisite temporal resolution. Moreover, ERPs can be used to examine both exogenous (acoustic representation) and endogenous (attention and learning) aspects of sound processing. ERPs are comprised of positive and negative deflections (i.e., waves) that reflect activation from neural ensembles involved in the processing of sensory information and can be used to assess how acoustic information ascends the auditory system from the cochlea to higher auditory cortical areas. The sequence of ERPs can be divided into early brainstem auditory responses (occurring between 1 and 10 ms after sound onset), middle-latency responses (occurring between 10 and 50 ms) and long latency responses occurring after 50 ms post-stimulus. Each deflection is identified according to its polarity, order of occurrence and/or latency. For example, the P1-N1-P2 cortical response consists of a small positive wave (P1), a large negative component (N1), followed by a positive peak (P2). The N1 peak, also referred to as the N100, is a negative peak that occurs

approximately 100 ms following sound onset (Figure 1). For long duration sounds (e.g., greater than 500 ms), the P1-N1-P2 is followed by a sustained potential and an offset response.

Cortical evoked responses such as those recorded in the middle- and long-latency ranges result from stimulus-locked post-synaptic potentials within apical dendrites of pyramidal neurons in the cerebral cortex. The extra-cellular electric currents spread through the conductive brain tissue, the cerebrospinal fluid, the skull, and the skin and result in voltage differences at the scalp surface, which are recorded using electrodes placed on the scalp. The number of recruited neurons, extent of neuronal activation, and synchrony of the neural response all contribute to the resulting pattern. The amplitude of ERPs can be used as an index of the strength of the response in microvolts (μV) whereas the latency refers to the amount of time, in milliseconds (ms), that it takes to generate

the bioelectrical response following stimulus onset. Latency is therefore related to neural conduction time and site of excitation: the time it takes for the sound to travel through the peripheral auditory system to the place of excitation in the central auditory system. Even though they are not routinely utilized in clinical settings, long latency ERPs are regularly used in research to determine how physical acoustic energy translates into patterns of brain activity and contributes to perception in normal and hearing impaired listeners (readers interested in learning more about recording and analysis of auditory ERPs should consult Burkard et al., 2006).

Scalp recorded ERPs have been instrumental in identifying physiological correlates underlying sensory processing and low-level auditory scene analysis. As previously mentioned, low-level scene analysis refers to those processes that are thought to occur automatically, independ-
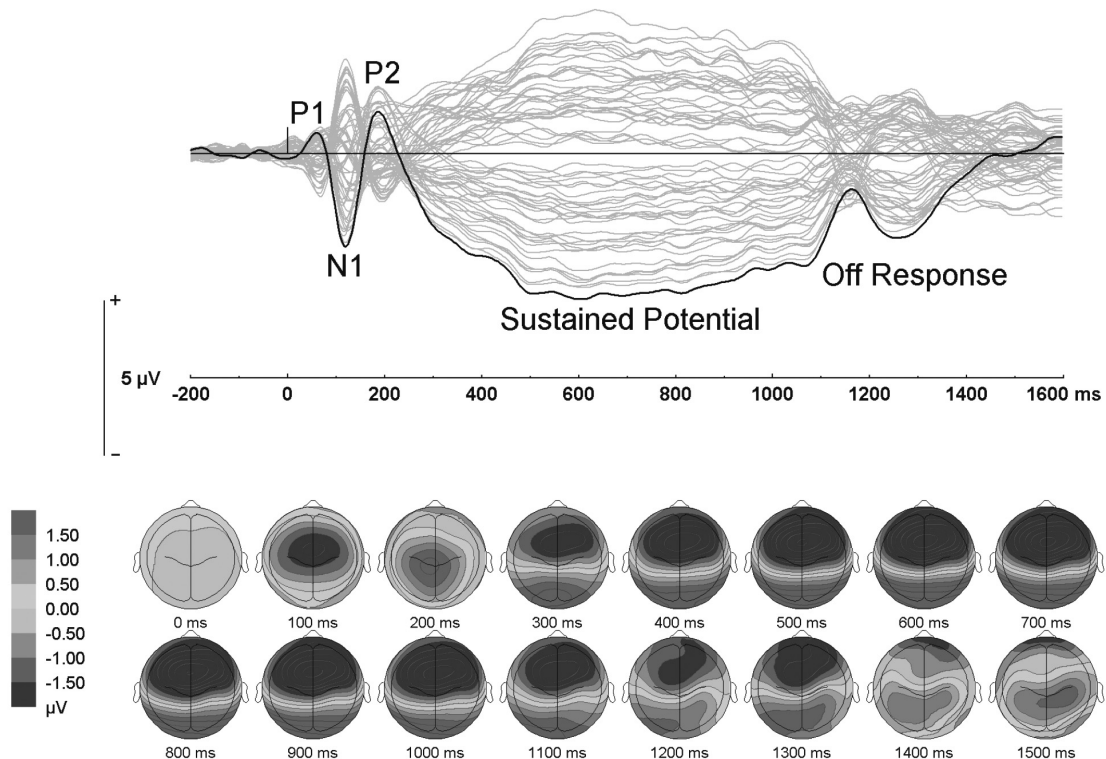

Figure 1. Butterfly plots illustrating the P1-N1-P2 evoked response elicited by sound onset as well as the sustained potential elicited for long duration sounds from 65 scalp electrodes. Each gray line reflects an evoked response recorded at one electrode. The black trace reflects activity recorded at the midline central electrode (Cz). Sound duration was 1000 ms. The amplitude distribution of the auditory evoked response is illustrated using contour plots (bird's eye view) at various latencies starting at time 0 and for every 100 ms steps until 1500 ms after stimulus onset. The darker areas indicate negative voltages whereas the lighter areas indicate positive voltages. Adapted from Alain et al. (2002).

ent of listener attention. This level of scene analysis requires that acoustic energy first be detected and then discriminated so that acoustic information can be either separated into distinct auditory events (e.g., words, musical notes) or grouped into one coherent stream or objects. Therefore, in the following sections, we focus on ERP correlates of sound detection and discrimination as well as for stream segregation and concurrent sound perception. More specifically, we focus our attention on three neuropsychological events occurring between 30 and 260 ms post-stimulus; namely the P1-N1-P2 complex, the mismatch negativity (MMN) wave, and the object-related negativity (ORN) wave, which have been associated with listeners' ability to detect, discriminate, and segregate concurrent sounds, respectively.

Physiological Detection of Sound

P1-N1-P2 responses are generated by multiple sources, including thalamo-cortical projections as well as primary and association areas of each auditory cortex (Picton et al., 1999). They are classified as "obligatory" responses because they represent the physiological detection of sound, and as it is assumed that sounds must first be detected before they can be discriminated, grouped, and ultimately perceived. The physiological detection of sound, and the effects of decreased audibility, has typically been examined by either varying the signal-to-noise ratio (Martin et al., 1997; Whiting et al., 1998; Martin and Boothroyd, 1999; Martin and Stapells, 2005), or testing individuals with sensory-neural (Ponton et al., 1996; Oates et al., 2002; Tremblay et al., 2003a) and conductive hearing losses (Vasama and Makela, 1997). Martin and colleagues, for example, examined the effects of competing signals by presenting speech signals embedded in noise (Martin et al., 1997; Martin and Stapells, 2005). They found that speech identification abilities decreased at poorer signal-to-noise ratios and the decrement in performance was paralleled by both increased N1 latencies and decreased N1 amplitudes. Similar ERP findings have been reported in people with hearing loss. Peak latencies are typically delayed,

and peak amplitudes smaller, when stimulus audibility is compromised by the presence of conductive or sensorineural hearing loss. Collectively, these results demonstrate that the typical person with a hearing loss, or when a person is trying to hear a signal in the presence of competing noise, is at a biological disadvantage. The physiological detection of sound in these circumstances is much slower and weaker than that of a person with normal hearing, listening in a quiet environment. More importantly, the amplitude and latency of N1 correlates significantly with behavioral assessment of signal detectability (Martin et al., 1997), with electrophysiological thresholds closely approximating behavioral thresholds (Lightfoot and Kennedy, 2006). These findings suggest that cortical auditory evoked responses provide a sensitive measure of signal audibility, which may prove useful in evaluating hearing function in those individuals that could not otherwise be tested with conventional behavioral techniques.

The P1-N1-P2 complex is sensitive to various stimulus parameters such as frequency (Naatanen et al., 1988; Woods et al., 1993), location (McEvoy et al., 1990; McEvoy et al., 1991), duration (Alain et al., 1997; Ostroff et al., 2003), and/or intensity (Taub and Raab, 1969). This sensitivity to variation in acoustic attributes makes it an ideal tool to examine the physiological detection of important acoustic cues contained within a signal. When evoked by the naturally produced speech sound /sei/, for example, the resultant waveform is comprised of multiple overlapping P1-N1-P2 responses signaling the onset of the consonant and vowel portions of the stimulus (Ostroff et al., 1998). As shown in Figure 2, the first N1 peak corresponded in time to the onset of the consonant /s/ (a change from silence to sound), while the onset of the second set of P1- N1-P2 peaks corresponds to the onset of the vowel /i/ (the consonant-vowel transition). Because different speech sounds evoke different neural response patterns (Tremblay et al., 2003b) and the presence or absence of N1 and P2 responses show a reasonable agreement with perceptual thresholds (Martin et al., 2006), there is growing interest in using the P1-N1-P2 complex to examine the neural representa-

tion of speech in individuals with communication disorders. For instance, abnormal speech evoked P1-N1-P2 responses have been reported in various populations with impaired speech-sound perception, including individuals with auditory neuropathy (Kraus et al., 2000; Rance et al., 2002), children with auditory based learning problems (Cunningham et al., 2000; Purdy et al., 2002) and aging adults (Tremblay et al., 2003a; Tremblay et al., 2004; Harkrider et al., 2005). Cortical auditory evoked potentials have also been recorded in people who wear cochlear implants (Ponton et al., 1996; Friesen and Tremblay, 2006) or hearing aids (Tremblay et al., 2006a), making it possible to examine the effects of improved signal audibility on the physiological detection of sound.

There is interest in using ERPs to determine if specific acoustic information is being detected physiologically in normal or hearing-impaired individuals. Because the P1-N1-P2 complex is relatively easy to record and shows good test-retest reliability, it could make an excellent tool for assessing central auditory processing, and might even someday help audiologists fit hearing aids and cochlear implants. This is important given that the P1-N1-P2 complex can be recorded without overt behavioral responses, allowing for the assessment of perceptual function in individuals that either cannot communicate or have difficulties understanding task instructions (e.g., children, aphasic or demented patients).

To summarize, the P1-N1-P2 complex is an ERP that signifies the physiological detection of audible stimulus energy and, from this perspective, can be seen as indexing the capacity for perception of this sound. Moreover, the P1-N1-P2 complex can be used to indirectly assess the integrity of the central auditory system, up to the cortex. The presence of a P1-N1-P2 response implies that a sound has reached the level of the cortex and is now available for further processing. In turn, abnormal or absent P1-N1-P2 responses suggest that the neural conduction of sound at the level of, or before, the cortex is in some way impaired. Referring back to our case example, this means, even if the businessman is fit with a hearing aid, to improve the audibility of sound, successful rehabilitation also requires that the CEO's voice be physiologically detected and discriminated, despite the presence of background noise, and that this auditory
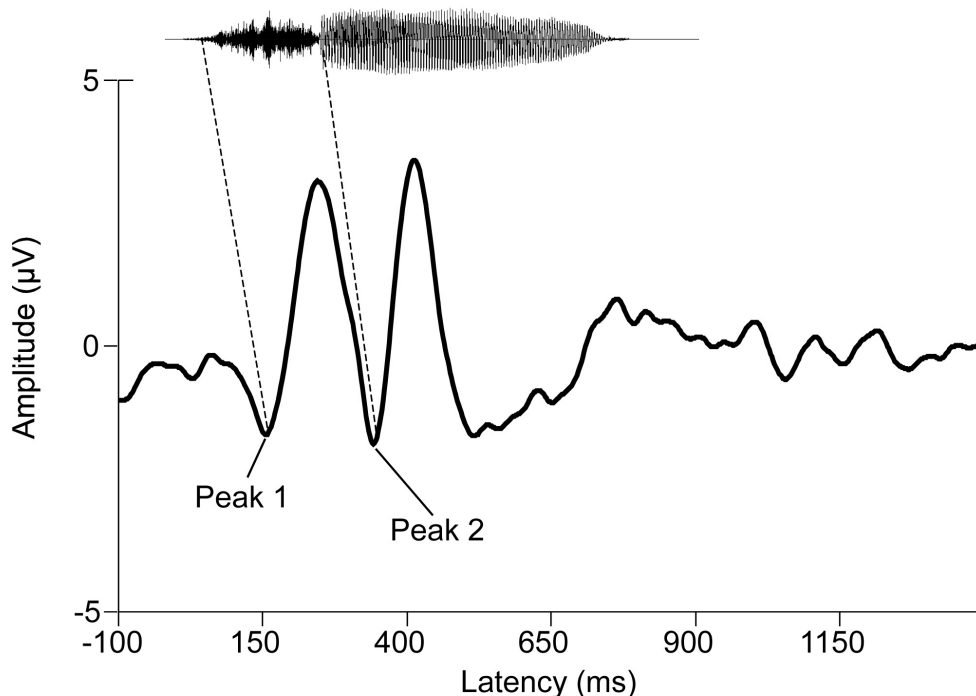

Figure 2. An auditory evoked response elicited by the speech token /ʃi/. Two P1-N1-P2 responses are present. The first N1 (Peak 1) corresponds to consonant onset, and the second N1 (Peak 2) corresponds to vowel onset. The overlaid acoustic waveform demonstrates the correspondence to the ERP waveform (adapted from Tremblay et al, 2006a).

input be processed at higher levels in the auditory system.

Physiological Discrimination of Acoustic Events

The physiological detection of acoustic cues contained within a stimulus is just one step in auditory processing. In order to perceive the difference between two words (e.g., "bee" and "pea"), listeners must also be able to discriminate the acoustic/physical differences between the two sounds (e.g., /b/ vs /p/). Without this ability, a person could easily confuse the two sounds and in turn misunderstand what is being said (e.g., confusing the word "bee" and "pea").

The ability to discriminate between stimuli has been investigated extensively using the mismatch negativity (MMN) wave. The MMN is typically evoked using an oddball paradigm where an acoustically "deviant" stimulus (e.g., "pea") is inserted in a series of frequently occurring simi-

Figure 3. Group mean ERPs from an oddball paradigm using gap (deviant) and no-gap (standard) stimuli in a group of healthy young adults. The top panel shows the ERP recorded over the right central scalp region (i.e., C4) while the bottom panel shows the corresponding difference wave between the ERPs elicited by the standard and the deviant stimuli. Adapted from Alain et al. (2004).

lar stimuli (e.g., "bee"). Other examples of stimulus contrasts include having frequent and deviant stimuli that differ along a physical dimension such as frequency, intensity, or spatial location (Picton et al., 2000; Kujala et al., 2006). The MMN can also be recorded to deviations in complex sound sequences, such as sounds that alternate regularly in pitch with occasional repetition (Alain et al., 1994; Alain et al., 1999). The MMN appears as a negativity in response to the deviant stimulus, approximately 100 to 300 ms post stimulus onset (Figure 3). "Obligatory" P1-N1-P2 responses are evoked simultaneously with the MMN because the deviants must first be detected before they can be discriminated. The MMN is best illustrated by computing a difference wave between the ERP elicited by the standard and the deviant sounds.

The MMN is described as a discriminative response because it presumably reflects the physical mismatch between a memory trace of the frequently occurring stimuli and the distinguishing acoustics of the deviant stimuli. MMN amplitudes increase and latencies decrease, as the deviant stimulus becomes more discriminable (Sams et al., 1985; Alain et al., 1994; Javitt et al., 1998; Alain et al., 2004). The effect of deviant discriminability is illustrated in Figure 4. In that particular study, participants were presented with occasional deviant sounds that included a small gap. The increase in gap duration was associated with improvement in gap detection and was paralleled by increase in MMN amplitude (Alain et al., 2004). Thus, the MMN can be said to reflect acoustic discrimination and auditory sensory memory (Picton et al., 2000; Naatanen et al., 2005).

Similar to earlier responses (e.g., P1-N1-P2), the MMN is recorded passively, without requiring the participant to attend or participate in a task. For this reason, the MMN became a popular tool for assessing biological processes underlying auditory perception in populations that are unable to reliably complete behavioral tests of perception. For instance, the MMN wave has been used to assess auditory function in older adults with cognitive impairments (Kazmerski et al., 1997), stroke (Alho et al., 1994; Alain
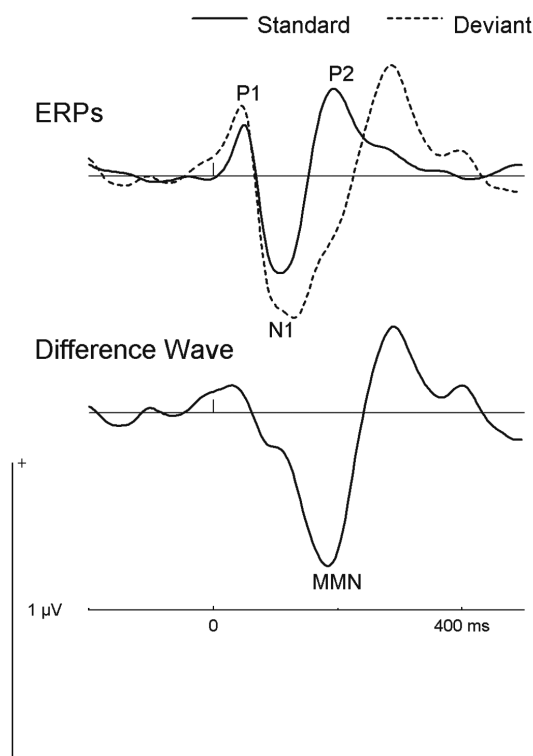
et al., 1998; Deouell et al., 2000), as well as children with attention, learning, and language disabilities (Kurtzberg et al., 1995; Kraus et al., 1996). More recently, the MMN paradigm has been used to show specific deficits in discriminating speech stimuli in left-hemisphere stroke patients with aphasia (Ilvonen et al., 2004).

Returning to the typical example of an audiology patient, it is not surprising that the presence of hearing loss, resulting in decreased stimulus audibility, also affects the ability to discriminate spectral and temporal differences between one or more sounds. Like the P1-N1-P2 response, reducing stimulus audibility through the use of masking increases MMN latency and decreases MMN amplitude (Martin et al., 1999), suggesting that decreased hearing sensitivity interferes with the ability to discriminate between standard and deviant stimuli. For this reason, when testing older adults, low-frequency stimulus contrasts have been used (i.e., 800 Hz tone as the standard stimulus and 552 Hz as the deviant stimuli) to minimize the confounding effects of age-related high-frequency hearing loss. Even when this method is used, age-

related changes in the MMN have been observed (Alain and Woods, 1999; Gaeta et al., 2002), especially when the stimuli are presented with a long inter-stimulus interval (Pekkonen et al., 1996), suggesting that the physiological discrimination of acoustic change is compromised in older adults. More recently, Alain and colleagues measured the MMN in young, middle-aged and older adults and found a decrease in MMN amplitude with increasing age, which remained even after controlling for age differences in discriminability (Alain et al., 2004). In other words, while young, middle-aged and older adults could detect the deviant stimuli to the same extent during an active listening task, older adults showed, nonetheless, a marked reduction in MMN amplitude (Figure 5). This is important because it indicates that some of the hearing problems experienced by older adults are related to deficits in central auditory processing as well as decreased audibility resulting from age-related hearing loss.

In summary, the MMN reflects the central auditory system's remarkable ability to register small occasional changes in
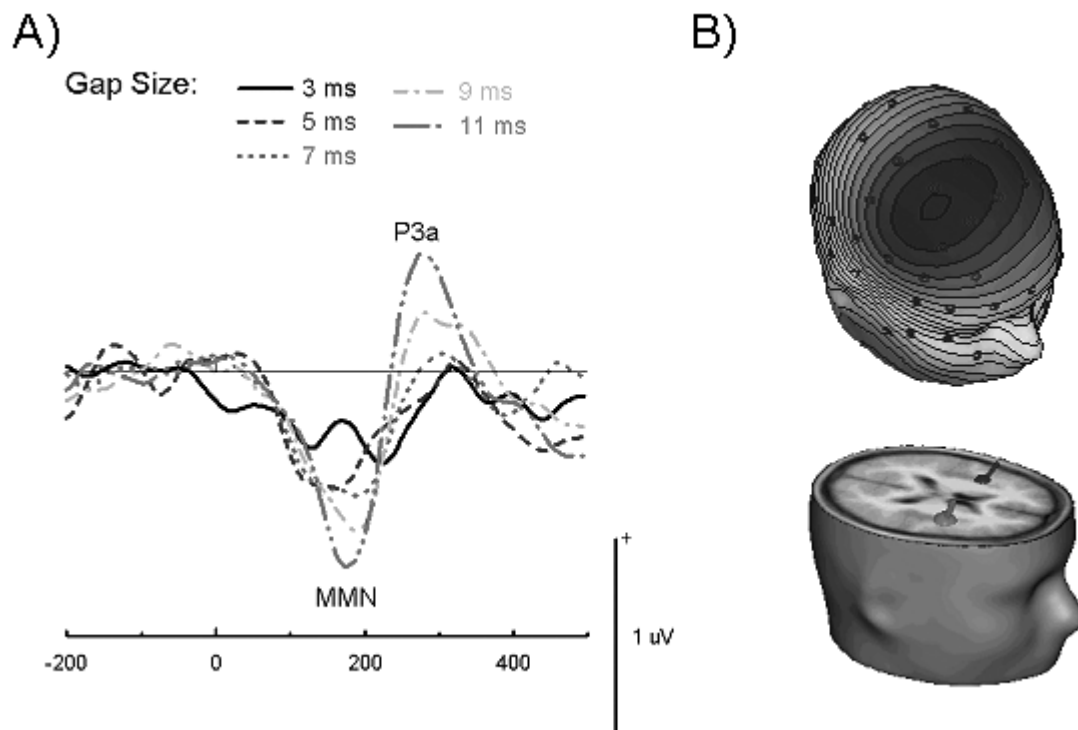

Figure 4. Effects of deviant discriminability on MMN amplitude: (A) group mean MMN recorded for various gap sizes; (B) contour maps (bird's eye view) illustrating the MMN amplitude distribution for the largest gap size along with the dipole source location. The darker areas indicate negative voltage. Adapted from Alain et al. (2004).
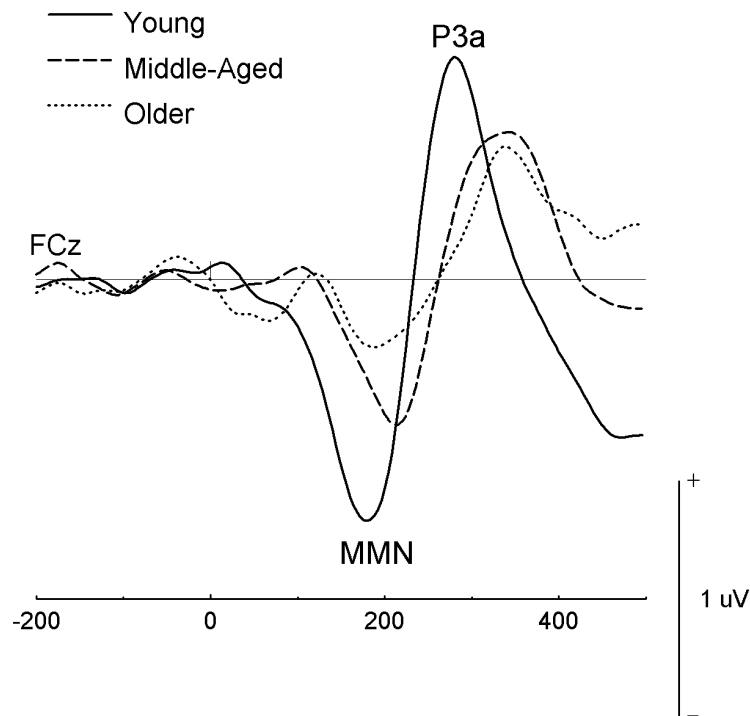
Figure 5. Effects of age on the MMN amplitude. Group mean MMN from young, middle-aged and older adults from the midline frontocentral electrode (FCz). The MMN reflect the grand average over all gap size. Note the reduced MMN amplitude in middle-aged and older adults despite equivalent performance during the auditory discrimination task. Adapted from Alain et al. (2004).

the perceptual stream. Our review of the literature shows that MMN amplitude is highly sensitive to discrimination deficits in different clinical populations including individuals suffering from learning disabilities and/or hearing impairment. For example, the MMN can be used to assess the functional status of auditory cortex in people with hearing loss and who wear cochlear implants (Kraus et al., 1993; Ponton and Don, 1995; Singh et al., 2004; Kelly et al., 2005; Roman et al., 2005; Singh et al., 2006). Moreover, in healthy young adults near threshold stimuli can elicit reliable MMN responses (Alain et al., 2004). For these reasons, there was (and still is) hope that the MMN could be used as a clinical tool for assessing central auditory discrimination. Moreover, new recording paradigms that provide the opportunity to profile different auditory discrimination abilities within a very short recording time are being developed (Naatanen et al., 2004). From a clinician's point of view, however, it is not only important to reduce testing time, it is also imperative that the sensitivity and specificity of the MMN be known

and that normative data be established. Because these requirements have not yet been met, the MMN is not routinely used in clinical settings.

Synthesis of Acoustic Information

Although sound detection and discrimination are prerequisites to subsequent perception of complex signals such as speech and music, the latter also depends on a collection of processes involved in sorting out the incoming acoustic data such that accurate representation of the physical acoustic world can be built and maintained in memory. The neural correlates underlying auditory scene analysis are receiving increasing attention due in part to the recognition that hearing involves more than just signal detection, it also requires that sounds be organized in a meaningful way. For example, auditory scene analysis can be described as the process whereby the brain assigns parts of the acoustic signal, derived from an amalgamation of physical sound sources, into perceptual objects (such as words or notes)
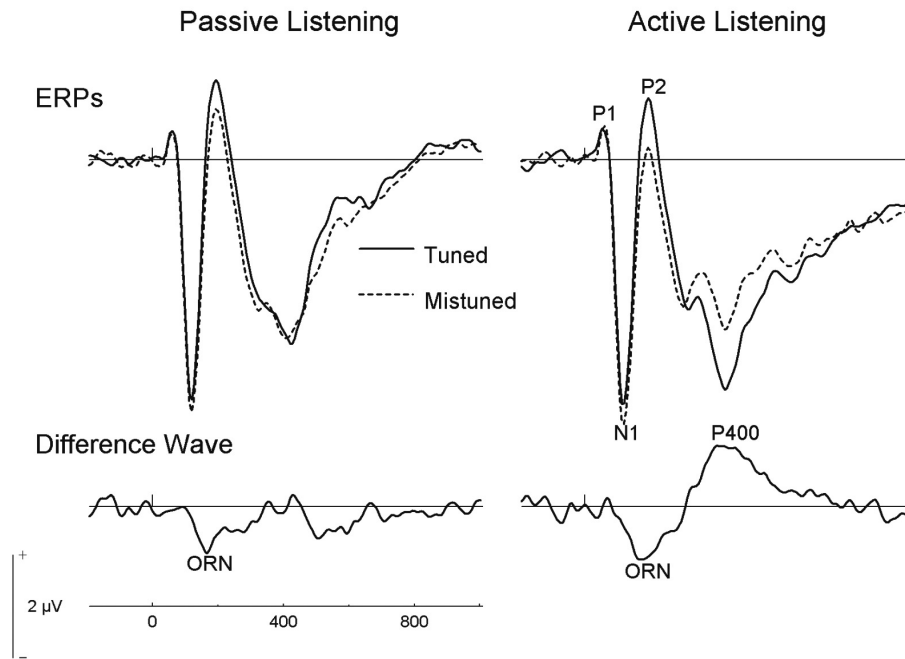
Figure 6. Object-related negativity (ORN). Group mean ERPs elicited by tuned and mistuned stimuli and the corresponding difference wave in a group of healthy young adults. Note that the ORN is recorded during both passive (i.e., participants read a book of their choice and no response was required) and active listening (response required). P400 wave was present only when participants were required to report whether they heard one complex sound or whether they heard a buzz-like sound plus another sound with a pure tone quality. The ORN and P400 amplitude correlated with listeners' likelihood of reporting hearing concurrent auditory objects. Adapted from Alain et al. (2001).

or streams (such as ongoing speech or music). In other words, the ability to "hear" certain events depends on listeners' ability to perceptually organize sounds that occur simultaneously and sequentially.

The neural correlates of concurrent sound perception were first examined using the mistuned harmonic paradigm (Alain et al., 2001; Alain et al., 2002; Dyson and Alain, 2004). In this paradigm, participants are presented with complex sounds comprised of tonal elements that are either all integer multiples of the f_0 (tuned stimulus) or comprise one tonal element that is not an integer multiple of the f_0 (mistuned stimulus). When all tonal elements are harmonically related, listeners usually report hearing one sound. However, if a low tonal component is not harmonically related to the sound's f_0 by about 4% or more of its original value, then listeners report hearing two concurrent sounds (Moore et al., 1986; Alain et al., 2001). In terms of phenomenology, the tuned stimulus often sounds like a "buzz" with a pitch corresponding to the f_0 whereas the complex sound containing a low partial mistuned by 4% (or more) contains the "buzz" element plus a separate sound with a pure-tone quality at the frequency of the mistuned harmonic. In this regard, a sound that has a different f_0 from other concurrent sounds (i.e., the mistuned harmonic) might signal the presence of another sound source (i.e., object) within the auditory scene. With respect to our example mentioned earlier, this may translate into hearing the voice of the group leader against the fan of the video-display and the overhead ventilation system. The auditory system is thought to achieve this type of perceptual organization by means of a harmonic "sieve" (Moore et al., 1986) or 'template' (Hartmann et al., 1990). When a portion of acoustic energy is mistuned to a sufficient degree, a discrepancy occurs between the perceived frequency and that expected on the basis of the template, signaling to higher auditory and cognitive centers that multiple auditory objects are present.

Alain and colleagues (Alain et al., 2001; Alain et al., 2002) found that the perception of the mistuned harmonic as a separate object was paralleled by a negative wave over frontocentral scalp sites that

peak at about 150 ms after sound onset. This negativity was referred to as the object-related negativity (ORN) because it correlated with listeners' likelihood of reporting hearing two concurrent sounds (Figure 6). The ORN is superimposed on the N1 and P2 elicited by sound onset, and therefore, is best illustrated by computing a difference wave between ERPs elicited by sounds that are perceived as one object from those that are heard as two concurrent sounds. Its amplitude and latency are minimally affected by attention (Alain and Izenberg, 2003; Dyson et al., 2005), suggesting that it indexes a pre-attentive process and that concurrent sound segregation operates independently of conscious control.

The ORN is not limited to the detection of mistuned harmonics; it can also be recorded when concurrent sounds are segregated based on location cues. For example, Johnson et al. measured late cortical potentials associated with the perception of dichotic pitch (Johnson et al., 2003). Dichotic pitch stimuli were created by introducing a dichotic delay to a narrow frequency region of the same noise segment, and resulted in perception of both the centrally-located noise and a right-lateralized pitch. In a recent study, McDonald and Alain (2005) found that observers were more likely to report hearing two concurrent auditory objects if the tonal component, either in tune or slightly mistuned (2%), was presented at a different location than the remaining harmonic. Interestingly, this was paralleled by an ORN that was present only when the tonal component was presented at a different location than the remaining harmonics. These results indicate that listeners can segregate sounds based on harmonicity or location alone, and that the conjunction of harmonicity and location cues contributes to sound segregation primarily when harmonicity is ambiguous. Taken together these findings suggest that the ORN reflects neural mechanisms involved in auditory scene analysis that can use a broad range of cues when parsing simultaneous acoustic events. This also suggests that this ERP components index the perception of concurrent auditory objects (e.g., voice, noise from the projector and the ventilation system) that results from combining various acoustic features into a perceptual object.

Another example of concurrent sound segregation that to some extent overcomes the artificiality of the mistuned harmonic, or the dichotic pitches paradigm, is the double-vowel task. The benefit of this task is that it provides a more direct assessment of speech separation, and also evokes the processes involved in acoustic identification, as opposed to detection. Here, listeners are presented with a mixture of two phonetically different synthetic vowels, either having the same or different f_0, and are required to indicate which two vowels are presented. Psychophysical studies have shown that the identification rate improves with increasing separation between the f_0 of the two vowels (Chalikia and Bregman, 1989; Assmann and Summerfield, 1990; Chalikia and Bregman, 1993; Assmann and Summerfield, 1994). Increased accuracy is paralleled by an ORN that reflects the Δf_0 differences between the two vowels, and peaks at about 150 ms after the onset of the double-vowel stimuli (Alain et al., 2005). As for the mistuned stimuli, this negativity is present in both attend and ignore conditions, consistent with the proposal that concurrent vowel segregation involves an early attention-independent process. The ORN was markedly reduced in a group of older adults who also experienced difficulties in parsing and identifying concurrent vowels (Snyder and Alain, 2005). Interestingly, young and older adults showed comparable amplitude for a more posterior and right-lateralized negative wave at 250 ms (N2b). This pattern of neural events supports a multistage model of auditory scene analysis in which the spectral pattern of each vowel constituent is automatically extracted and then matched against representations of those vowels in working memory. It also suggests that older adults may recruit additional resources, or rely more on top-down schema-driven processes, reflected in the N2b, in solving the scene analysis problem.

Previous works have shown that the ORN can be recorded in children (Alain et al., 2003) and older adults (Snyder and Alain, 2005). However, to our knowledge, no one has used the ORN in clinical populations. Such ERP components may be helpful in investigating listeners' abilities to process acoustic cues critical for sound segregation. Given that its recording does not require listeners' participation, it can be used to assess

concurrent sound segregation in children and patients with language problems. Further research is also needed to clarify the link between concurrent sound perception, as measured by either the mistuned harmonic paradigm or the double-vowel task, and speech perception.

For our businessman to understand what is being said at the meeting, he must not only be able to separate sounds that occur simultaneously but he must also be able to keep the flow of incoming information into separate streams of sounds such that he can extract the meaning of what is being said. This second form of primitive grouping takes place along the time axis, and auditory streaming acts as a striking psychophysical demonstration of how sequential sound segregation works. In a typical experiment, participants are presented with ABA— ABA— sequences in which "A" and "B" are sinusoidal tones of different frequencies and "—" is a silent interval. The frequency separation between the A and B tones is manipulated to promote either the perception of a single gallop-like rhythm (ABA— ABA—) or the perception of two distinct perceptual streams (A—A—A—A— and B——B——), with the beat of the A tones being twice that of the B tones (as indicated by longer ——). Listeners are required to indicate when they can no longer hear the two tones as separate streams but instead hear a single galloping rhythm. The fusion or coherence boundary refers to the frequency separation where individuals perceive a single stream of sounds with a galloping rhythm, whereas the fission or segregation boundary refers to the point where listeners can no longer hear the galloping rhythm and report hearing the sounds as coming from two separate sources. The area between fusion and fission boundaries is typically ambiguous and leads to a bistable percept in which listeners' perception alternates between hearing the sounds with a galloping rhythm and hearing two concurrent streams.

Gutschalk et al. (2004) used magnetoencephalography (MEG) to record evoked responses to ABA— patterns in which the frequency separation and presentation rate was manipulated in a standard streaming paradigm. P1 and N1 responses, time locked to the B tone and arising from primary and/or secondary auditory cortex on the superior temporal plane, increased with fre-quency separation. The increase occurred at larger frequency separations for the slower presentation rate, which is consistent with the necessity of larger frequency separations to hear streaming at slower presentation rates. In a second experiment, participants listened to extended sequences of repeating ABA— patterns and indicated by pressing a button when their perception switched from one stream to two streams or vice versa. Separate averages of the MEG data, according to their perceptual state, revealed small additional increases in the P1, N1, or P2 responses when participants perceived two streams compared to one stream. This is an important finding because it suggests that changes in P1-N1-P2 are not solely reflecting the difference in frequency between the A and B tones (i.e., delta-F) but appear to be linked to perception.

Using EEG, Snyder et al (2006) found similar frequency-separation-related increases in the P1-N1-P2 responses at frontocentral scalp locations in response ABA— patterns. When comparing neural activity for different repetitions of the ABA— patterns, they found a positive enhancement of activity at frontocentral scalp locations that peaked about 200 ms after the beginning of each repetition of the ABA— pattern, paralleling the perceptual buildup of streaming that occurs over several seconds. In addition to the activity at frontocentral locations, they also observed increases in ERP amplitude as the frequency difference between the A and B tones increased as well as a gradual increase in amplitude from the beginning to the end of the sequence that mimics the build-up of stream segregation over time at temporal electrodes but only on the right side, suggesting hemispheric asymmetry for stream segregation. Measurements were made during two separate experimental sessions with the same participants. In one condition, participants were actively attending to the sounds and indicating whether they heard one stream or two streams by the end of the sequence of ABA— patterns. In the other condition, they ignored the ABA— patterns and watched a subtitled muted movie of their choice. Ignoring the ABA— patterns had little effect on the P1-N1-P2 modulation related to frequency separation, whereas it markedly reduced the positive activity that increased during the course of the 27 ABA— repetitions. These

data suggest that attention effects on stream segregation observed in perceptual tasks (Carlyon et al., 2001) are due to effects on perceptually linking temporally separated tones of the same frequency into a coherent stream rather than on the initial separation of tones of different frequencies.

As for the concurrent sound perception, few studies have examined the relation between sequential stream segregation and speech perception in normal or hearing-impaired listeners. Rose and Moore (1997) showed that bilaterally hearing impaired listeners required greater frequency separation than normal hearing listeners for stream segregation to occur. Moreover, the impact of hearing loss on sequential stream segregation has been observed in a number of other studies using a similar paradigm to that of Rose and Moore (Grimault et al., 2001; Mackersie et al., 2001; Mackersie, 2003). Stainsby, Moore, and Glasberg (2004) showed that hearing-impaired listeners could segregate sounds using temporal cues, and suggested that stream segregation does not depend solely on the frequency resolution of the peripheral auditory system.

FINAL THOUGHTS

Hearing is a dynamic process that requires detecting, discriminating, grouping, and separating incoming sounds into meaningful units. Using the scene analysis framework enables scientists and clinicians to bridge various areas of hearing research that encompass signal detection and the formation of more abstract representations of our auditory environment. Moreover, it provides a framework for describing normal and disordered processing.

Although taken for granted, perception of speech and music are highly complex signals that involve interactions between peripheral and central auditory processing. It is likely to be the interaction between low-level and high-level mechanisms that leads to successful speech identification in adverse listening situations since primitive grouping mechanisms alone are not sufficient to fully account for perceptual organization of speech (Remez et al., 1994). This point is also probably true for people with hearing disorders and should therefore be kept in mind when discussing auditory rehabilitation.

Traditional approaches to rehabilitation once included intervention measures geared to low-level (e.g., improving signal audibility with the use of hearing aids or other assistive listening devices) and high-level (e.g., speech reading, auditory visual integration and other types of auditory training exercises) processing. However, over time, reimbursement for rehabilitative services became more difficult so the focus of audiology clinics shifted more to dispensing hearing aids and away from teaching patients how to "hear" with the device. But, as described by Pichora-Fuller and Singh (2006), higher level functions such as attention, cognition and memory play important roles in successful communication, and long-standing approaches to rehabilitative audiology should be revitalized to emphasize the important role that training and therapy play in promoting compensatory brain reorganization. For instance, animal (e.g., Recanzone et al., 1993; Weinberger, 2004) and human (e.g., Tremblay et al., 2001; Reinke et al., 2003; Bosnyak et al., 2004) studies have demonstrated that the biological representation of sound can be modified with focused listening training exercises. Most importantly, training/learning-related changes in physiology have been shown to coincide with improved perception. For this reason, ERPs have been used to explore similar phenomena in humans and the P1-N1-P2 and MMN responses, for instance, have been used to track neuroplastic changes associated with an improvement in auditory discrimination. A common finding is that peak responses become larger and shorter in latency as perception improves (for a review see Tremblay, 2007).

For all of the above-mentioned reasons, there is increasing interest in learning more about the physiological processes underlying perception. With this information, we might better understand why a person, like the businessman in our case example, has difficulty hearing at work; why a hearing aid might be extremely helpful for one person but not another; or why an assistive listening devices (such as an FM system) can be more helpful than a hearing aid when listening in a noisy environment. For instance, it might be that one person's auditory system is more efficient than another at separating simultaneous signals (speaker's voice and background noise) while

wearing a hearing aid. Perhaps another person requires an FM system that automatically enhances the desired signal and attenuates competing noise in a way that their own auditory system cannot.

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