Speech Sound Representation in the Brain

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Key Words

Speech perception · Speech sounds · Neural
representation · Auditory evoked response · Children ·
Mismatch negativity (MMN)

Abstract

Biologic processes underlying speech sound perception
and learning have been addressed using the mismatch
negativity (MMN) evoked response. First is a consider-
ation of how the acoustic properties of the signal affect
the neural mechanisms and brain regions engaged. Be-
cause the MMN differs depending on the acoustic char-
acteristics of the stimuli used to elicit the response, it has
been used to probe mechanisms underlying the neural
representation of stimuli along the auditory pathway.
Second is a consideration of neurophysiologic correlates
of speech sound perception and learning. Detailed is
a 'behavioral-neurophysiologic, acoustic-phonetic ap-
proach', used to link perception with underlying physio-
logic processes in humans. The focus here is on children
and what has been learned about normal maturation of
speech sound perception and its disruption in certain
children with learning disorders. The last topic is a con-
sideration of central nervous system changes with per-
ceptual learning. This includes long-term experience
with one's native language and short-term auditory
training in the laboratory. Limitations and future chal-
lenges are discussed.

Introduction

Objective measures of brain function, such as evoked
potentials and neural imaging, have been useful in estab-
lishing basic structure-function relationships in the hu-
man auditory system. For example, certain evoked re-
sponses have been linked to aspects of auditory percep-
tion and activity within the auditory cortex, the auditory
brainstem and the auditory periphery. Neural imaging
has also revealed the activity of certain brain areas during
auditory perception. Moreover, abnormal images and
electrophysiologic responses have perceptual correlates.
But beyond these broad relationships, our knowledge of
how objective measures reflect specific aspects of audito-
ry function and perception is still rudimentary.

The aspect of auditory function considered here is
speech sound perception and its biologic underpinnings.
Measures of perception are available behaviorally, al-
though the measures inherently reflect cognitive and lin-
guistic factors. We know little about the biologic processes

underlying fine-grained auditory perception and even less about the biology of preconscious sensory processes. A link between fine-grained perceptual abilities and physiologic processes is needed to better link perception with its physiologic roots and to improve clinical measures of perception and learning.

The mismatch negativity (MMN) is special because it is one of few such existing measures that can provide such a link. The aspect of speech sound processing that the MMN represents can be thought of as *central sensory representation* of speech sounds which occurs after peripheral sensory encoding and largely independently of conscious perception (attention and cognition). The MMN is a powerful tool for understanding neural mechanisms underlying speech perception for the following reasons: (1) it is a neurophysiologic reflection of just perceptible acoustic differences; (2) it reflects the representation of dynamic properties of the speech signal – the inherently changing sound structure of speech; (3) its role in echoic memory processes is particularly relevant to speech, because it may underlie processes which make it possible to keep in memory what is being said while listening to speech in real time; (4) it reflects dynamic neural properties of the brain; (5) with respect to more long-term dynamic processes, it is modifiable with learning and experience over time; (6) importantly, the MMN reflects preconscious stimulus processing – it can be distinguished from attention/motivation/cognitive factors.

These advantages have motivated scientists to use this response despite the difficulties encountered – most notably its variability in individual subjects.

At Northwestern University, we take a combined behavioral-neurophysiologic, acoustic-phonetic approach to the investigation of biologic processes involved in speech sound perception. Because we can define characteristic acoustic correlates of major speech sound classes, we can manipulate these acoustic parameters to focus specifically on parameters that are known to bear critical speech information and thereby begin to pinpoint the exact nature and origin of auditory deficits that may affect communication. The relationship among the listener's perception of acoustic signals, the neurophysiologic representation of those same signals and other behavioral measures of speech perception and language processing is examined in order to link perception of speech to underlying central physiological processes [Kraus et al., 1996, 1999; Koch et al., 1999; Carrell et al., 1999; Luce and Pisoni, 1998]. The experimental approach consists of obtaining these measures *in the same person.* In a complementary animal model, intracranial responses *to the same stimuli* used in the human studies are obtained to gain insight into generating sources and neural mechanisms involved in the representation of these sounds in the brain [Kraus et al., 1994a, b; McGee et al., 1996; King et al., 1999]. Specifically, by examining the MMN to elemental acoustic speech contrasts, we have gained insight into mechanisms underlying normal speech perception and perceptual deficits in clinical populations, relevant also to treatment strategies.

What follows is a summary of how the mismatch response has been used to learn about biologic processes underlying speech sound perception and learning. First, how the acoustic properties of the signal affect the neural mechanisms/generating sources engaged is considered. Second, studies that have linked acoustic-phonetic perception with underlying physiologic processes in humans are reviewed. The focus is on children and what has been learned about normal maturation of speech sound perception and its disruption in certain children with learning disorders. The last topic is a consideration of how the central nervous system changes with perceptual learning, including long-term experience with one's native language and short-term auditory training in laboratory or clinical environments.

Neural Mechanisms Vary with the Acoustic Properties of the Signal

The mismatch response has been recorded at multiple levels of the auditory pathway – midbrain, thalamus, cortex, with distinct contributions by right and left sides, nonprimary and primary pathways. In humans, generating sources inferred from scalp recordings have included the auditory cortex [Giard et al., 1990; Hari et al., 1984] and frontal cortex [Giard et al., 1990; Näätänen and Michie, 1979]. Direct intracranial recording supports auditory cortex contribution [Kropotov et al., 1995].

Intracranial recording in animals has revealed MMN in the hippocampus [Csépe et al., 1987; 1989], auditory midbrain [King et al., 1995], auditory thalamus and cortex [Kraus et al., 1994a, b; King et al., 1995; Javitt et al., 1992]. To our knowledge, there have been no attempts to record MMN from auditory structures more peripheral to the midbrain. An open question is whether a representation of stimulus change reflected by MMN occurs at lower levels of the system.

The MMN appears to have a strong extralemniscal (nonprimary) pathway origin. Specifically, dipole source analysis is consistent with nonprimary auditory cortex

contributions [Scherg and Picton, 1990]. Moreover, the MMN was recorded from the nonprimary auditory thalamus, not the primary subdivision [Kraus et al., 1994a; King et al., 1995]. The role of nonprimary pathways in auditory learning and CNS plasticity has been demonstrated by numerous single neuron experiments [Edeline and Weinberger, 1991]. The nonprimary pathway origin of the MMN is consistent with MMN changes that accompany perceptual learning (reviewed below).

Different Pathways Depending on the Stimulus

Acoustic parameters are represented differently along the auditory pathway (e.g., representation of periodicity in steady-state signals diminishes in progressively more central regions along the auditory pathway) [Creutzfeldt et al., 1980]. We have long known that in humans with auditory processing problems and central pathway lesions, the perception of acoustic contrast is not uniformly impaired, with some sounds being more or less vulnerable to disruption. Phillips and Farmer [1990] reviewed a series of reports in which cortical damage affected the processing of rapid acoustic transitions which characterize certain consonants but did not affect the perception of slowly changing signals. Children with learning problems may have difficulty discriminating certain sounds (e.g., /ba-pa/, /ba-da/, /da-ta/, /da-ga/, /ɛ-æ/) while the perception of other sounds is less affected (e.g., /ba-wa/, /a-i/) [Kraus et al., 1996; Mody et al., 1997; Reed, 1989; Tallal and Piercy, 1974, 1975; Brandt and Rosen, 1980; Godfrey et al., 1981; DeWeirdt, 1988; Elliot et al., 1989; Sussman, 1993].

The MMN has revealed that the involvement of specific pathways depends on the stimuli used to elicit the response. This is important because it becomes possible to evaluate the contribution of distinct brain regions and mechanisms to the neural and perceptual processing of various acoustic characteristics. Topographic and spatiotemporal modeling studies demonstrate that the MMN is generated by different supratemporal areas in response to acoustic changes in frequency, intensity and duration [Alho et al., 1996; Giard et al., 1995; Tiitinen et al., 1993]. In addition, different magnetic MMN dipole sources for frequency changes occurring within complex sounds are different from those for the same frequency change in simple tones, suggesting that simple and complex sounds are processed in different regions of the auditory cortex [Alho et al., 1996].

Returning to speech stimuli, when MMNs are recorded from within thalamic and cortical structures in the guinea pig, an interesting differentiation of responses occurs depending on the stimulus [Kraus et al., 1994b]. The physiologic representations of the contrasts /da-ga/ and /ba-wa/ were examined. The synthesized /da-ga/ contrast varied only in the onset frequency of the third formant, while formant transition duration was varied for /ba-wa/. These stimuli were used because, as mentioned above, the perception of the place of articulation (ba-da-ga) is known to be vulnerable to mis-perception in people with perceptual deficits. In the animal model, any acoustic change resulted in a mismatch response that could be recorded from the cortical surface (i.e. yielded an epidural MMN). However, intracranial recording in the auditory thalamus showed a mismatch response to the /ba-wa/ contrast but not to the /da-ga/ contrast. The contribution of the auditory cortex appears to be required for the representation of the /da-ga/ acoustic difference.

Hemispheric Symmetry

Right versus left hemisphere specialization also seems to depend on the acoustic characteristics of the stimulus. The MMN elicited by tones is larger over the right hemisphere (in both children and adults), irrespective of the ear stimulated [Giard et al., 1990; Korpilahti and Lang, 1994; Paavilainen et al., 1991; Csépe, 1995]. However, in response to speech stimuli, the MMN can be symmetric both in adults [Aaltonen et al., 1994; Tremblay et al., 1997] and throughout the school-age years [Kraus et al., 1999].

Other studies in adults have shown that speech-elicited MMNs can be asymmetric. Csépe [1995] reported that MMNs elicited by vowels were slightly larger over the right hemisphere, while MMNs to stop consonants had maximum amplitude over the left hemisphere. Likewise Alho et al. [1998] have shown that MMNs elicited by syllables (standard /da/, deviants /di/ and /ba/) were larger over the left hemisphere. Moreover, while MMNs elicited by nonnative speech syllables were initially symmetric, responses became especially enhanced over the left hemisphere following training [Tremblay et al., 1997]. In addition, the MMN elicited by the syllable /da/ was larger over the left hemisphere when /da/ signaled a phonetic change but was symmetric when the same /da/ signaled a pitch change [Sharma and Kraus, 1995]. Näätänen et al. [1997] also found left hemisphere enhancement to phonetically relevant native language prototypes. It appears that the

linguistic or phonetic nature of speech stimuli as well as the specific acoustic-phonetic sound structure influence the hemisphere more actively in discriminating stimulus change.

Acoustic Context Matters

The neurophysiologic response elicited by an identical stimulus may evoke the contribution of different neural sources depending on the acoustic context in which it occurs. For example, the stimulus /da/ was perceived and represented differently topographically depending on the acoustic context in which it was presented. In one context, /da/ signaled a pitch change (/da/-high vs. /da/-low), in another a phonetic change (/da-ga/) [Sharma and Kraus, 1995]. Similarly, in a patient with a left temporal lobe lesion, behavioral perception of the same pitch change was normal; however, his perception of the phonetic contrast was severely impaired. Consistent with his behavioral perception, MMN was apparent when /da/ signaled a pitch contrast and absent to /da/ when it signaled a phonetic difference [Sharma et al., 1994; Kraus et al., 1995b]. Similarly, Alho et al. [1996] found that the same frequency change activated different magnetic MMN source locations depending on whether it occurred in a simple tonal sequence or within a complex sound (chord or serial sound pattern).

In summary, the MMN has been used to further our understanding of neural representation of sound in the brain. The representation of acoustic change is evident in auditory pathway structures (midbrain, thalamus, cortex – especially nonprimary subdivisions) and nonauditory areas (frontal cortex and hippocampus). The involvement of specific pathways depends on the acoustic and phonetic characteristics of the stimuli. The auditory pathway shows a specialization of processing such that certain acoustic discriminations require processing at the cortical level. MMN to the *same* stimulus evokes different generating sources/mechanisms depending on the acoustic context in which the acoustic change occurs. The same acoustic change invokes different generating sources/echoic memory mechanisms depending on whether it occurs within the context of simple versus complex sound stimuli. Responses to speech stimuli are complex, and appear to reflect (1) the physical features of the signal, (2) the acoustic context in which stimuli are presented and (3) the individuals' perceptual experience with the signal as speech.

Linking Speech Perception with Underlying Physiologic Processes

Acoustic-Phonetic Representation

Linking speech perception with underlying biologic processes can be done when physiologic and related behavioral measures are obtained in the same individual. In this section, we focus on experiments in which this is the case. A link between speech sound discrimination and perception was made when it was demonstrated that MMN could be obtained not only in response to easily discriminable changes in speech stimuli, but also to changes at the psychophysical discrimination threshold [Kraus et al., 1992, 1993; Ceponiene et al., 1999]. Although the MMN is not a direct measure of discrimination, these results are consistent with the view that the MMN is associated with fine-grained perceptual discrimination processes.

While behavioral and physiologic responses are related in that they reflect processing of acoustic events, it must be remembered that these are inherently different responses. Psychophysiological tasks require a conscious, behavioral response. In contrast, the neurophysiologic response is a preattentive neural representation of acoustic change, originating largely within the auditory pathway, and does not depend on attention or a voluntary response. Nevertheless, they reflect intersecting processes, providing insight into processes that operate separately and together.

Maturation

An important question is the extent to which the perception and neurophysiologic representation of certain speech sounds changes with age. Overall, the MMN develops early, particularly compared to other cortical evoked responses [Courchesne, 1990], and may be the ontogenically earliest discriminative response of the human brain [Cheour-Luhtanen et al., 1996]. It has been recorded in preterm infants (30–34 weeks), neonates and awake 3-month-old infants [Cheour-Luhtanen et al., 1995, 1997]. While MMNs in school-age children and adults are quite similar, considerable evidence suggests that the MMN differs in infants and school-age children in latency, amplitude and topography [Aaltonen et al., 1987; Cheour-Luhtanen et al., 1995, 1996, 1997; Cheour et al., 1998a, b; Alho, 1995; Leppänen et al., 1997]. No information exists on MMN development in preschool children.

Neurophysiologic and psychophysical measures of speech sound discrimination have been used in school-age

children ranging in age from 6 to 16 years [Kraus et al., 1999]. Fine-grained acoustic-phonetic discrimination abilities (just noticeable differences) were obtained from 134 children for synthesized stimuli along /da/ to /ga/ and /ba/ to /wa/ continua which ranged from easy to hard to discriminate. The data indicated that both the perceptual and physiologic measures were already mature by the age of 6 years and did not change during the school-age period. There were no differences in either measure between male and female children, and the MMN was symmetric over temporal and frontal lobes throughout the entire age range studied. Beyond providing information about the normal development of these perceptual processes, these data provide a metric for comparison of children with perceptual deficits. The fact that MMN detectability, onset latency, area and duration are stable during this age period facilitates the application of this response in studies involving normal children and various clinical populations. This large-scale study is consistent with previous MMN studies in school-age children [Csépe, 1995; Kraus et al., 1992, 1993], although a somewhat different developmental pattern has been observed to tonal contrasts [Kurtzberg et al., 1995]. This difference underscores the fact that developmental patterns cannot be expected to generalize to all stimuli, because different MMN-generating sources may be engaged depending on the sound structure of the signal used to elicit the response. Importantly, the aforementioned physiologic experiments are consistent with psychophysical experiments, indicating that the perception of speech sounds is largely mature in school-age children [Allen and Wightman, 1992; Bargones et al., 1995; Jensen and Neff, 1993; Nittrouer, 1992, 1996; Nittrouer and Studdert-Kennedy, 1987; Olsho, 1985; Trehub et al., 1995; Walley et al., 1984].

Learning Disorders

School-Age Children. Kraus et al. [1996, 1999] have hypothesized that speech sound perception problems may arise (at least in some cases) from faulty neural representation in central auditory centers. Presumably, these acoustic-level disorders are abnormalities in the *central sensory representation* of speech stimuli that occurs after peripheral sensory encoding and prior to conscious perception (which involves attention and higher-order cognitive processes).

The Listening, Learning and the Brain Project ongoing at Northwestern University is an investigation of auditory function at a basic elemental acoustic level in normal and learning-disabled children. An overall goal is to understand the biologic basis for the sound perception deficits found in some children with learning problems. Other goals are to better understand which acoustic-phonetic elements provoke perceptual difficulties and to apply this knowledge to improve speech sound training strategies. From a clinical standpoint, an aim is to develop an objective way to identify those children who have deficits in acoustic-level encoding and to determine whether intervention in the form of speech discrimination training will help. A focus of the experiments is to examine the relationship among psychophysical speech discrimination (listening), standardized measures of learning and academic achievement (learning) and neurophysiology (the brain) in a large population of both normal and impaired children. To date, over 500 children are enrolled in the project.

As reviewed above, behavioral data have shown that a subset of children with diagnosed learning problems exhibit deficits perceiving certain speech sounds. An interesting relationship emerged between the neurophysiologic representation and the behavioral discrimination of selected speech sounds. Kraus et al. [1996] wanted to determine whether these difficulties originate from abnormalities in the neurophysiologic representation of acoustic events prior to conscious perception in addition to/or separate from higher-level processing deficits. They investigated how 90 children with learning problems and 91 healthy controls discriminated fine-grained differences along two 40-step speech continua (/da-ga/ and /ba-wa/) in a task involving conscious decision making [Carrell et al., 1999]. Children with learning problems demonstrated a diminished ability to discriminate contrasts only along the /da-ga/ continuum, which was related with a diminished magnitude of the MMN. These results indicate a biologic basis for some children's perceptual deficits, originating in the auditory pathway before conscious perception. The selective impairment of neural representation and behavioral discrimination of the /da-ga/ pair in contrast to the /ba-wa/ pair is consistent with the view that the representation of certain acoustic elements has distinct auditory pathway origins and is differentially vulnerable to disruption.

Pursuing further the question of what precise acoustic-phonetic features provoke perceptual difficulties, Bradlow et al. [in press] examined whether lengthening the consonant-vowel formant transition duration from 40 to 80 ms would result in improved discrimination thresholds for children with poor just noticeable differences along a /da/-to-/ga/ continuum. Discrimination thresholds remained significantly elevated in the children with

learning problems irrespective of formant transition length. Consistent with earlier findings, children with learning problems had significantly smaller MMNs to the short-transition /da-ga/ contrasts compared to normal children. Interestingly, however, in children with learning problems, MMNs to the longer-transition stimuli were larger than the responses to the shorter-duration stimuli. Normally learning children had equivalent responses to both short- and long-transition stimuli. Thus, whereas lengthening the formant transition duration did not enhance perceptual discrimination, the electrophysiologic data indicated that, at a preconscious level, the long-transition duration stimuli were better represented than the short-transition duration stimuli in the subjects with learning problems.

It is conceivable that the better neurophysiologic representation of the longer-duration stimuli may underlie the success of training strategies which employ stimuli with lengthened formant transitions [Merzenich et al., 1996; Tallal et al., 1996]. Brief-duration stimuli – which are poorly represented physiologically by the auditory CNS – may be difficult for children to access during the learning process. Taken together, the behavioral and neurophysiologic data suggest that the source of the underlying perceptual deficit may be a combination of faulty stimulus encoding at a neural level and deficient representation at an acoustic-phonetic level.

In summary, the following relationships between fine-grained speech perception and neurophysiologic representation of the same signals (as reflected by MMN) have emerged. Speech sound discrimination and underlying neurophysiologic representation may be present at birth and are largely mature by school age. Neurophysiologic responses reflect speech sound perception abilities in normal children and children with learning problems. There appears to be a biologic basis for certain selective speech sound perception deficits, with deficits occurring, at least in part, at a preconscious level.

If children with impaired central sensory representation of speech sounds could be identified, one would be in a better position to recommend appropriate therapeutic strategies. Because this perceptual system is highly modifiable with perceptual learning (see below), it is likely that these children would benefit from therapeutic approaches employing perceptual learning.

Applications in Infants and Preschool Children. An important aspect of MMN is that it can reveal information about sensory perception without requiring behavioral participation, making it amenable to research and clinical applications. Although this review of MMN has focused on studies in which both behavioral and neurophysiologic data were available, a few studies performed in infants (without behavioral data) bear mentioning. A genetic basis for dyslexia has been well documented [Pennington, 1995]. The MMN has been shown to be distinctive in infants at risk for dyslexia as compared to infants with a negative family history for dyslexia [Leppänen and Lyytinen, 1997]. Moreover, language and speech deficits and learning problems also are commonly reported in children with various syndromal conditions. Perceptual deficits based on an abnormal MMN have been demonstrated in children with velocardiofacial syndrome (microdeletion of chromosome 22, characterized by e.g. cleft palate, cardiac anomalies and learning problems) [Haapanen and Somer, 1993; Kok and Solman, 1995]. In addition, MMN is attenuated not only in school-age children with cleft palate but is already attenuated in newborns born with cleft palate [Cheour et al., 1999]. Thus, MMN may reflect risk factors for learning difficulties (and their underlying nature) long before they are manifested in school performance.

Other Speech-Related Phenomena

Comodulation Masking Release and McGurk Effect

The MMN has yielded physiologic data regarding psychophysical perceptual processes relevant to speech perception including comodulation masking release or CMR [King, 1996; Hall et al., 1984] and the McGurk effect [McGurk and MacDonald, 1976]. The CMR is relevant to our ability to hear signals in a noisy background. In this paradigm, tones are presented either in amplitude-modulated noise (comodulated) or in noise bands differing in amplitude modulation (conflicting). Perceptually, a tone is easier to hear when presented in comodulated noise because the amplitude modulation is used to group auditory signals together. In guinea pigs, MMNs were obtained in the midbrain, thalamus and cortical surface in the comodulated condition, but not to the same stimuli with conflicting modulation. Thus, the MMN reflected improved tone salience characterized by CMR and indicated that a neural correlate of CMR is evident at the level of the auditory midbrain [King et al., 1995].

The McGurk effect demonstrates a perceptual fusion between auditory and visual (lip-read) information in speech perception under the condition of audiovisual discrepancy created by dubbed video tapes [McGurk and MacDonald, 1976]. That is, the same speech syllable can be perceived differently depending on the accompanying

visual-speech cues. Sams et al. [1991] demonstrated a neural representation of stimulus change (magnetic MMN) elicited by identical speech sounds when the 'deviant' stimulus had discrepant visual cues. Thus, visual information of articulatory movements seems to have an entry into the auditory cortex.

Speech Sound Perceptual Learning

Speech perception abilities in humans can be modified both by long-term experience with one's native language and with more short-term, auditory training like that which occurs in a laboratory or clinical environment. Experiments using MMN have provided insight into both aspects of perceptual learning: native language experience and auditory training.

Native Language Experience

According to numerous psychological studies [Aslin et al., 1981; Jusczyk, 1985; Kuhl, 1987; Mehler, 1985; Treuhub, 1976; Werker, 1989; Werker and Lalonde, 1988; Werker et al., 1981], infants are born with a capacity to discriminate phonetic contrasts in any of the world's languages. This ability is affected by (long-term) experience with one's native language. Within the first year of life, perceptual abilities become 'tuned' to sounds used in the child's native language [Kuhl et al., 1992; Werker and Polka, 1993; Werker et al., 1992]. Moreover, there appear to be critical periods during which it is easier to learn to discriminate and perceive these native language sounds [Snow and Hoefnagel-Hohle, 1987].

If the auditory system changes with speech sound experience, it might be hypothesized that sounds that occur in one's native language would be better represented biologically than nonnative sounds. Näätänen et al. [1997] compared MMN responses in Finnish and Estonian subjects to the vowel /õ/ which exists (is a prototype) in Estonian but not in Finnish. Consistent with their language experience, physiologic responses (MMNs) were significantly larger to that vowel in Estonian subjects than in Finns. Another interesting finding from this study is that speech sound experience also appears to affect hemispheric dominance – the relative representation of that sound in the two hemispheres. In Finns, the prototype /o/ elicits a significantly larger MMN in the left than in the right hemisphere, whereas responses to nonprototype /õ/ were small and quite similar in amplitude in both hemispheres.

The developmental changes in infants' abilities to discriminate native and nonnative contrasts have been demonstrated in numerous behavioral studies (see above). Neurophysiologic data have revealed that language-specific memory traces develop within the first year of life [Cheour et al., 1998b] and are evident as early as 3 months of age [Dehaine-Lambertz and Baillet, 1996]. In the former study, MMN amplitude reflected only the acoustical difference between the deviant and standard stimuli, in 6-month-old Finnish infants. That is, the MMN was larger for the Estonian than for the Finnish prototype. However, by 1 year of age, the MMN was attenuated in Finnish infants in response to the Estonian vowel. In contrast, Estonian 1-year-olds showed almost equally large MMNs to both vowels, both of which are Estonian prototypes. Importantly, these results also showed that MMN amplitude for Finnish vowels increased in Finnish infants between 6 months and 1 year of age. Thus, by 1 year, not only have children's abilities to perceive non-native vowels diminished, but perception of native vowels has improved.

Auditory Training

Speech sound perception can be modified by directed auditory training. This typically consists of short-term training in a laboratory environment. Training sessions tend to be about 1 h in duration, occurring over a few weeks or months. Psychophysical studies have shown that adult listeners can be trained to discriminate sounds not used in their native language [Pisoni et al., 1982; Bradlow et al., 1997]. For example, experiments have involved training Japanese speakers to distinguish between /r/ and /l/. Moreover, it has been demonstrated that speech perception can be modified by auditory training in language-impaired children [Bradley and Bryant 1983; Tallal et al., 1996; Merzenich et al., 1996; Ball and Blachman, 1999; Shankweiler et al., 1995]. These behavioral studies indicate that speech perception abilities can be modified with training in both adults and children, and that training can generalize to other acoustic environments and to more real-life contexts.

Experiments using MMN have yielded insight into underlying neurophysiologic changes associated with perceptual learning. At Northwestern University, research has demonstrated that neurophysiologic changes associated with speech sound perceptual learning can be observed in humans [Kraus et al., 1995a]. Specifically, young normal-hearing adults were trained to discriminate just per-

ceptibly different variants of /da/ and /ga/. The subjects performed at chance level prior to training. After training, significant changes occurred in the MMN, with improvements in behavioral discrimination that were maintained 1 month after the last training session.

It was also important to determine whether training effects generalized to other speech sounds not used in training [Tremblay et al., 1997]. Using a psychophysical paradigm developed by McClaskey et al. [1983], normal-hearing English-speaking adults were trained to discriminate and identify a voicing contrast that does not occur in English but is phonetically salient in Hindi and Eastern Armenian. They were trained to hear that distinction of voice onset time in a bilabial context, but were evaluated before and after training on their ability to discriminate and identify the voicing contrast both in the bilabial context (training condition) and an alveolar context (transfer condition). After training, the subjects could identify and discriminate both the training and transfer contrasts behaviorally. Training and generalization effects were manifested by increases in MMN duration and area. Learning-associated neurophysiologic changes were more pronounced over the left than over the right frontal cortex. From a rehabilitative perspective, it may be that discrimination training for well-chosen acoustic elements of speech might generalize to other acoustic contexts.

There are remarkably few data on preconscious neural mechanisms of learning. Insight into biologic changes occurring during training (including preconscious processes) was gained by a combined assessment of behavioral and neurophysiologic responses throughout the course of training [Tremblay et al., 1998]. Neurophysiologic change was apparent *before* behavioral improvement was evident, suggesting that training altered the neural activity that underlies coding of acoustic events before those changes are integrated into conscious perception.

In summary, MMN is a human neurophysiologic response that reflects speech sound perceptual learning. It has revealed that experience with one's native language alters the central sensory representation of specific speech sounds. In addition, it has provided information about the plasticity of these processes in newborns as well as the time course of the development of sensitivity to sounds in one's native language. It is also apparent that short-term speech sound training alters the neural representation of acoustic events, including the generalization of learning to other acoustic stimuli not used in training. Moreover, neurophysiologic changes may be evident before learning is manifested behaviorally. Importantly, learning-associated neurophysiologic changes can be distinguished from and viewed in conjunction with behavioral learning which demands higher-level attention and cognitive processes.

MMN – Limitations/Future Directions

While it is evident that the MMN has been useful in furthering scientific knowledge about the biologic processes underlying speech sound perception in *groups* of subjects, its use in the assessment of *individuals* is limited by the variability of the response in individual subjects. Nevertheless, studies are systematically addressing the issue of test-retest reliability [Escera and Grau, 1996; Tervaniemi et al., 1999; Pekkonen et al., 1995; Frodl-Bauch et al., 1997]. Moreover, several laboratory groups are actively addressing ways to enhance the signal from background EEG activity and to improve the objective quantification of the response [Ponton et al., 1997; McGee et al., 1997; Lang et al., 1995; Joutsiniemi et al., 1998].

It will also become important to better understand the relationship of the MMN to speech sound perception. For example, an MMN may be present to stimuli that the subject does not perceive behaviorally. Conversely, the MMN can be absent from stimuli that are perceptible behaviorally. There are various explanations. For example, the MMN obtained to stimuli not behaviorally perceived may be due to motivational or perceptual factors which affect behavioral assessment. Moreover, the MMN may reflect perceptual abilities that are not consciously apparent. The case of an absent MMN to behaviorally perceptible stimuli may be the result of the poor signal/noise ratio of the response, or perhaps it is truly not generated by the brain. That is, conscious discrimination may not require processes responsible for MMN generation. Finally, it is important to realize that MMN and behavioral responses to the same signals represent *different* aspects of signal processing, the former being preattentive and neurobiologic while the latter involves the conscious integration of perceptual information. Where processes underlying the MMN and conscious perception intersect, as well as the separate processes they represent, they provide insight into the biologic and perceptual processes that govern how we hear speech.

It is presently unclear whether the MMN will be sufficiently reliable to be used in clinical applications involving individual subjects. Moreover, its precise relationship to behavioral perceptual processes remains illusive. However, as outlined at the outset of this article, the MMN is

one of few biologic indexes of fine-grained perception available. For this reason, it will likely continue to yield important new insights into speech sound processing in various research and clinical endeavors.

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