'Primitive intelligence' in the auditory cortex

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The everyday auditory environment consists of multiple simultaneously active sources with overlapping temporal and spectral acoustic properties. Despite the seemingly chaotic composite signal impinging on our ears, the resulting perception is of an orderly 'auditory scene' that is organized according to sources and auditory events, allowing us to select messages easily, recognize familiar sound patterns, and distinguish deviant or novel ones. Recent data suggest that these perceptual achievements are mainly based on processes of a cognitive nature ('sensory intelligence') in the auditory cortex. Even higher cognitive processes than previously thought, such as those that organize the auditory input, extract the common invariant patterns shared by a number of acoustically varying sounds, or anticipate the auditory events of the immediate future, occur at the level of sensory cortex (even when attention is not directed towards the sensory input).

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The role of the auditory cortex is usually understood in terms of sound perception and sensory memory, with higher (cognitive) processes operating on this sensory information at higher levels of brain organization. Bregman theorized that the perceptual organization of sound was handled by innate neural mechanisms operating at a pre-attentive level of processing[1], based on the results of several behavioral studies with infants[2] (see also Ref. 3) and adults[1]. However, because behavioral measures engage attentional mechanisms, it is difficult to determine the locus of these organizational processes on this basis alone. Recent neurophysiological evidence, however, suggests that many of these cognitive processes occur, in fact, in the auditory cortex. The evidence to support this new and more cognitive role of the auditory cortex largely originates from investigations using the mismatch negativity (MMN), which is mainly generated in the auditory cortex (Box 1). The results suggest that it is, in fact, the well-structured neural representation of the 'auditory scene'[1] that is involved (when violated by stimulus change) in MMN generation[4,5]. Different types of perceptual–cognitive achievements of central auditory processing (mainly occurring in the auditory cortex) are summarized in Table 1.

Central sound representation: underlying sound perception and transient sensory memory

On the basis of a large number of MMN studies, Näätänen and Winkler[6] have concluded that the neural traces involved in MMN generation in the auditory cortex encode the specific sensory information that appears in our auditory perception and sensory memory; that is, they carry the central sound representation (CSR). The authors have further proposed that the transient build-up phase of CSR underlies the perception of a (brief) sound and the slowly decaying phase of CSR the transient sensory memory of the sound.

Auditory change detection

The MMN data (reviewed in Box 1) suggest that the auditory cortex maintains the representation of the immediate auditory past. Furthermore, each sound is automatically compared with these representations, and if some of the regularities are violated, then MMN, which represents the difference signal, is generated (see Box 1). This auditory cortex process itself is pre-perceptual but tends to trigger frontal cortex activity (reflected by the frontal MMN subcomponent[7]), which probably underlies the initiation of attention switch to sound change[7,8].

Auditory stream formation and segregation

Typically, we receive acoustic information that originates from several simultaneous sound sources. Our central auditory system, therefore, has to segregate this mixture of the concurrent sound streams from each other and to attribute them to their original sources. The pitch, timbre, and location of the origin of the sounds, for example, provide cues used in stream segregation[1], which results in multiple perceptually separate sound streams. This process of assigning sensory inputs to the sound sources they belong to (that is, building a neural representation of the auditory environment) is called auditory stream segregation[1].

Auditory stream segregation occurs in the early, pre-attentive stages of auditory processing[9,10]. Sussman *et al.* have presented a sequence of alternating high- and low-pitched tones to subjects instructed to ignore the sounds and read a book[9]. Alternating tones at a slow pace are heard as a single stream of sounds that jump up and down in pitch. The rapid pace induces a streaming effect: the perceptual illusion that the tones form two independent concurrent streams of sound. Deviants in the fast – but not the slow-paced – conditions elicit MMNs. Thus, MMNs are elicited only when the tones split to separate streams, suggesting that in this fast-pace condition, the memory underlying MMN generation can maintain the information about the parallel streams separately, that is, the auditory stream

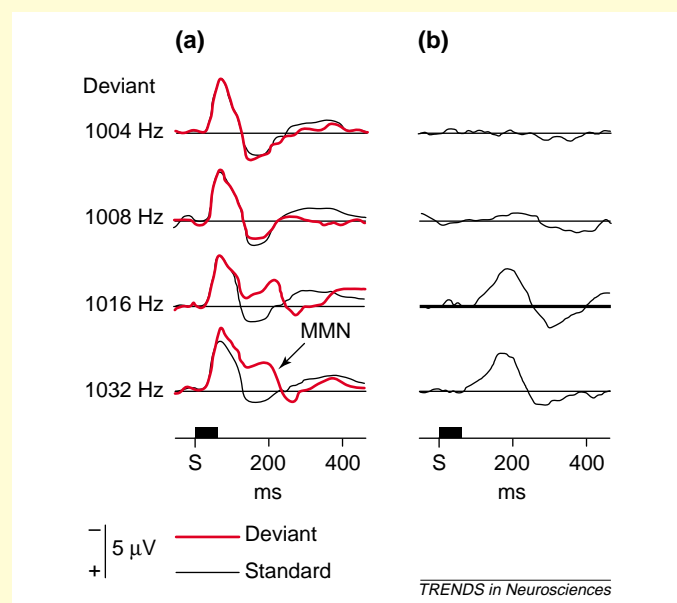## Box 1. The mismatch negativity

Fig. I. (a) Frontal (Fz) event-related potentials (ERPs) (averaged across subjects) to randomized 1000 Hz standard (80%, black line) and to deviant (20%, red line) stimuli of different frequencies (as indicated on the left side). (b) The difference-waves obtained by subtracting the standard stimulus ERP from that of the deviant stimulus for the different deviant stimuli are shown. Subjects were reading a book. Adapted, with permission, from Ref. b.

The mismatch negativity (MMN)[a] (and its magnetic equivalent MMNm) is elicited by any discriminable change in some repetitive aspect of auditory stimulation, irrespective of the direction of the subject's attention. This negative component of the auditory event-related potential (ERP), usually peaking 100–200 ms from change onset[b] (Fig. I), is based on, and reflects, neural traces by which the auditory cortex models the repetitive aspects of the acoustic past[c]. These traces might contain sensory information on

sound frequency, duration and inter-stimulus interval (ISI), but also on more complex aspects of auditory stimulation, such as rhythmic patterns or speech sounds[c]. The properties of these traces (which usually last several seconds, although even permanent traces can be reflected[c]) can be probed by presenting infrequent deviant events in the sequence of repetitive events ('standards')[c]. MMN is elicited even in the absence of attention, for example, in individuals in a coma a few days before the recovery of consciousness[d], which indicates that MMN indexes pre-attentive (attention-independent) auditory processing.

Currently, MMN provides the only objective measure of sound-discrimination accuracy[e]. There is a close relationship between the MMN amplitude and the discrimination accuracy[f]. Moreover, MMN can also be used to index the training-related improvement in discrimination ability[f]. Because of these properties, MMN has been successfully used in dyslexia research[g], for example, for evaluating the effectiveness of different training and rehabilitation programs. Other fields of the potential application of MMN include early language development[h], cochlear implants[i], schizophrenia[j], alcoholism[k], aging[l], Alzheimer's disease[m], and coma monitoring[n] and outcome prediction[o] (for a review, see Ref. p).

The main neural generators of MMN are bilaterally located in the supratemporal plane[q], which is indicated by dipole modeling[r] and scalp current density maps[s] of scalp-recorded event-related potentials, as well as by magnetic recordings[t], intracranial MMN recordings in cats[u], monkeys[v] and humans[w–y], and by positron emission tomography[z], functional magnetic resonance imaging[aa,bb], and optical imaging data[cc]. Furthermore, the exact locus of MMN in auditory cortex depends on the attribute[dd] (and even on the complexity of stimulus configuration[ee]) in which the change occurred. Therefore, one can conclude that the auditory processes that generate MMN originate, in the first place, in the auditory cortex. In addition, MMN also receives a contribution

segregation occurs in an early pre-attentive stage of auditory processing that precedes the stage of (automatic) MMN generation (see also Ref. 11). Nonetheless, top-down processing might affect the formation of auditory streams when the acoustic parameters allow multiple alternative organizations of the auditory input (ambiguous auditory scenes)[10].

Recent evidence indicates that auditory streaming takes precedence over temporal integration in the auditory cortex, as the ~200 ms temporal integration window, within which stimulus omissions elicit an MMN (Ref. 12), refers separately to each concurrent sound stream[13]. [MMN is elicited by sound omission in constant-rate sequences only when the stimulus onset asynchrony (SOA) <200 ms.]

Sound object formation
Sussman *et al.* have demonstrated pre-attentive auditory grouping within a single sound source[14]. They presented a repetitive sequence of five tones (AAAAB) at a slow pace to subjects who were ignoring the tones (SOA = 1.3 s). MMN was elicited by the

frequency-deviant B tone, but it disappeared when the tone sequence was presented at a fast pace (SOA = 100 ms). This suggests that the five tones were pre-attentively grouped together as a single perceptual unit, or sound object, when presented at the fast rate and, therefore, the B tone, being part of the unit, elicited no MMN. In contrast, with the slow presentation rate, the perceptual unit of stimulation was a single tone (A), and thus the B tones elicited MMN because they deviated from the more frequent tones.

Pre-attentive sound anticipation by transient extrapolatory traces
Even when subjects perform a task unrelated to the sound, MMN can be elicited by a steadily descending tone sequence that is interrupted by an ascending tone, and even by tone repetition[15] (Fig. 1). This result suggests that the auditory cortex does not only model the immediate auditory past but also forms extrapolatory traces on the basis of the regularities or trends detected in the auditory past,

from a (mainly right hemispheric) frontal generator that appears to be triggered by this auditory-cortex change-detection process and be associated with the initiation of attention switch to the change[ff].

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that is, these traces can represent anticipatory sound events[4,17].

Extracting abstract sound patterns from the ongoing stimulus sequence

Saarinen *et al.* presented tone pairs to their subjects when they were reading a book[18]. The standards were ascending pairs (that is, rising in frequency from the first to the second tone of the pair), whereas the deviant pairs were descending ones. Maintaining the frequency ratio between the first and second tone of the pairs, they randomly occurred on five different frequency levels, thus forming no physically constant standard pair, but rather a higher-order, 'abstract' standard, the direction of the tone pair *per se*. The descending tone pairs elicited MMN, indicating that the automatically formed memory records encode these abstractions (for example, an ascending pair; a case of simple concept formation) (see also Ref. 19).

Paavilainen *et al.* replicated these results under a more stringent control of attention[20], strengthening the conclusion that they indeed represented achievements of pre-attentive processing ('sensory intelligence'), rather than those of post-perceptual cognitive operations. Subjects were instructed to detect deviant tone pairs in one ear and to ignore stimulus pairs in a concurrent sound sequence presented to the opposite ear. MMN was nevertheless elicited by direction-deviant pairs, even in the ignored ear (however, only when this was the right ear), suggesting that it is the left hemisphere that is specialized in extracting possible abstract rules in acoustically varying input sequences.

Sound categorization on the basis of relationships between sound attributes

Very recently, Paavilainen *et al.* found that the pre-attentive sound analysis mechanisms are even capable of extracting invariant abstract relationships between two sound features[21]. Their standard stimuli continuously varied over a large range in frequency and intensity, so that there was no physically

Table 1. Perceptual–cognitive functions of the central auditory system

Process outcome	Function
Transient sensory-memory trace of a sound (central sound representation)	Sound perception and transient sensory memory (trace emergence and decay, respectively)
Auditory change signal	Auditory change detection
Sorting of multi-channel auditory input into sources	Auditory stream formation segregation
Temporal auditory grouping	Sound-object formation
Transient extrapolatory sound trace	Preattentive sound anticipation
Transient abstract sound-pattern trace	Perception and discrimination of abstract sound patterns
Transient representation of relations between sound attributes	Sound categorization on the basis of relations between sound attributes
Permanent sound trace	Recognition and discrimination of familiar sounds (e.g. voices, melodies, environmental sounds)
Permanent category-recognition sound trace	Permanent categorical sound perception (e.g. speech perception, key- and instrument-independent melody recognition)

constant, repetitive standard stimulus or feature conjunction. Instead, the various examplars of the 'standard' stimulus obeyed a rule such as 'the higher the frequency, the louder the intensity'. An occasional deviant stimulus (for example, a high-frequency soft stimulus) that violated this rule elicited MMN, demonstrating that pre-attentive auditory processing can detect abstract rules that govern the relationships between the different attributes composing a sound.

Permanent sound recognition and discrimination

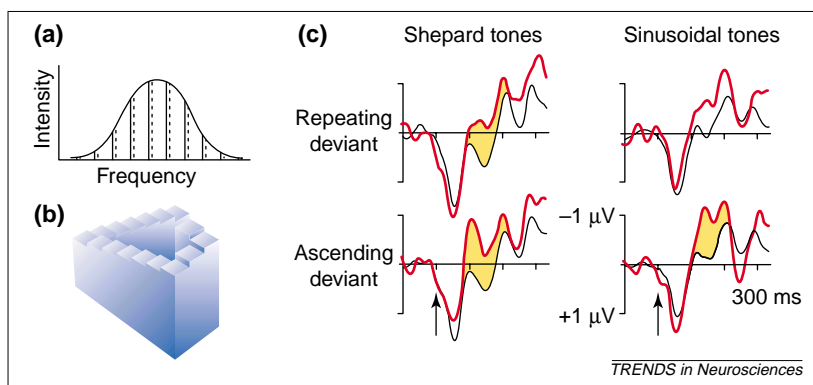MMN does not only reflect transient sensory traces but also more permanent ones. This is illustrated in

Fig. 1. (a) Spectrum of an individual Shepard sound that, when presented in ascending or descending sequences of 12 sounds in one semitone steps, causes a pitch to ascend or descend in an endless manner. One Shepard sound consists of ten frequency components, of one octave apart, with a bell-shaped spectrum. While a 12 tone series of Shepard sounds is delivered, the tone height (which is equivalent to the sense of octave) perception is made to disappear by manipulating the sound spectrum. (b) A visual analogy of the Shepard illusion, the endlessly ascending or descending stairs. (c) The event-related potentials recorded at the frontal (Fz) electrode from reading subjects to Shepard (left) and sinusoidal (right) tones (black line, standard stimulus; red line, deviant stimulus). The left column shows a regularly descending Shepard sound sequence randomly replaced by a repeating (top) or an ascending (bottom) tone (deviant). The arrow indicates the deviant-stimulus onset and the yellow area indicates the statistically significant part of the mismatch negativity. The right column shows the same for sinusoidal tones. Adapted, with permission, from Ref. 15.

Fig. 2, which shows that MMN that is not initially elicited by a change in a complex spectro–temporal pattern, develops in the course of the session, as subjects learn to discriminate these changes[22]. It appears that this MMN elicitation is due to the gradual development of an accurate enough representation, or trace, for the complex spectrotemporal pattern. (Consistent with this, the exogenous response to this stimulus pattern, similar to standard and deviants, remained very large throughout the session in those subjects who never learned to discriminate deviants from standards; for their auditory system, the standard stimulus seemed to be a 'new one' each time because of the failure to model it[22].) A subsequent study recording magnetoencephalogram (MEG) has shown that this type of MMN is generated in the auditory cortex[23]. Furthermore, using exactly the same stimuli, Atienza and Cantero have shown that this MMN training effect is present even in rapid eye movement sleep during the third night after the training[24].

Such presumably permanent traces probably serve as recognition patterns or templates for the corresponding stimuli in auditory perception[25]. They might explain, for example, the fact that we can immediately recognize a large number of different speakers on the phone. Interestingly, in the course of discrimination training, MMN might, in fact, emerge earlier than the subject is behaviorally able to discriminate the change[26].

Categorical sound perception guided by recognition traces (for example, speech perception)

The existence of language-specific memory traces (in the auditory cortex) was demonstrated by Näätänen *et al.*[27] (see also Ref. 28). They found that Finnish subjects' MMN to an occasional replacement of the repetitive Finnish (and Estonian) vowel /e/ was larger when the deviant sound was a vowel in Finnish (/ö/) than when it was a vowel in Estonian only (/õ/). By contrast, both deviant sounds elicited enhanced MMNs of about equal amplitude in Estonian subjects, in whose mother tongue both are vowels. The MEG recordings of the magnetic equivalent of MMN (MMNm) located the origin of the enhanced MMN to the Finnish vowel /ö/ in Finnish subjects to the left auditory cortex, which therefore appeared to accommodate the mother-tongue vowel-trace system (Fig. 3). A considerably smaller MMNm was in parallel generated in the right auditory cortex, which could be attributed to the (mere) acoustic deviance. For further MMN or MMNm evidence for permanent phonetic traces in the auditory cortex, see Refs 29,30.

The development of such permanent traces is probably a necessary pre-requisite for the correct perception of speech. These traces can accommodate, or normalize, variations across speakers (in, for example, timbre and pitch) and word context
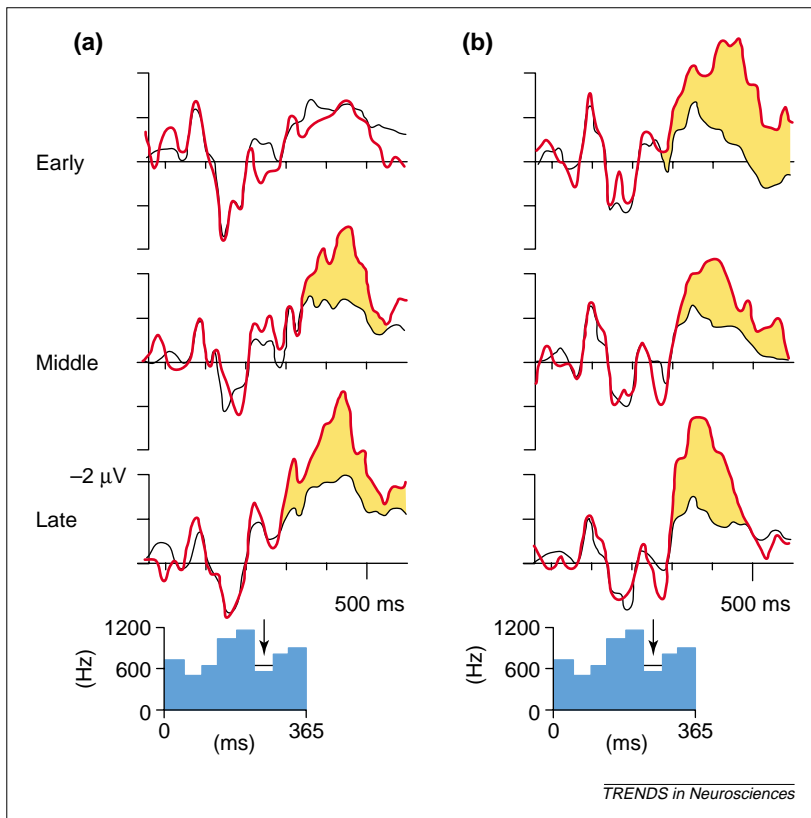
Fig. 2. (a) Grand-average vertex (Cz) event-related potentials (ERPs) of seven subjects reading a book to standard (black lines) and deviant (red lines) stimulus patterns during the early, middle and late mismatch negativity (MMN)-recording phases of the session. The performance of the subjects in the discrimination test after the early phase was weak but was considerably improved after the second and, in particular, the third phases. This improvement was accompanied by MMN (yellow area) emergence. The eight-segment stimulus pattern is schematically illustrated at the bottom of the figure. The only difference between the standard (sixth segment 565 Hz) and deviant (650 Hz) patterns is indicated by the arrow. (b) Corresponding data for those five subjects who were very good in discriminating deviants among standards, even after the early phase. They had MMN even in this early phase of the session. Adapted, with permission, from Ref. 22.

(allophonic variation) by carrying invariant codes that define the speech–sound categories shared by different speakers (and word contexts)[25,29,30].

Näätänen has proposed that an essential aspect of this invariant phoneme code for the vowels might be the F2:F1 ratio (with F2, and thus F1, remaining within a certain frequency range)[25]. Consistent with this, Paavilainen *et al.* have obtained results suggesting that the sound traces underlying MMN generation are also able to encode a constant frequency ratio of two parallel tones that widely vary in frequency[31]. Their MMN was elicited by violations of this frequency ratio, demonstrating the existence of such neuronal populations that might subserve vowel perception.

Concluding remarks
In summary, this article has reviewed MMN (and MMNm) evidence to suggest the existence of different forms of pre-attentive cognitive operations in audition. It is of considerable interest that these cognitive processes occur, mostly, at the level of the auditory cortex (most probably in the secondary and association areas[27,29,30]) where we can observe these
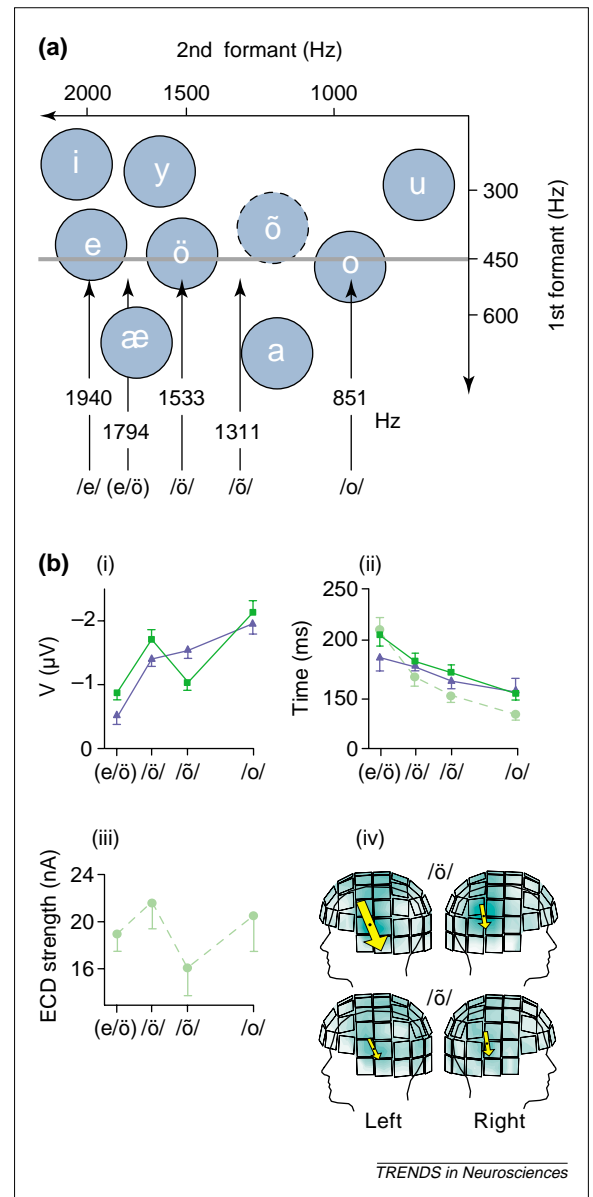
Fig. 3. (a) The arrows show the locations of the vowel stimuli in the F1–F2 space. The standard stimulus was the Finnish and Estonian prototype /e/; the deviant stimulus (e/ö) was an intermediate between /e/ and /ö/; the deviant stimulus /ö/ was a prototype shared by the two languages; the deviant stimulus /õ/ was an intermediate between the Finnish and Estonian prototypes /ö/ and /o/, and closely corresponded to the Estonian prototype /õ/; the deviant stimulus /o/ was a prototype in both languages. (b) (i) Mismatch negativity (MMN) peak amplitude (at frontal, Fz) in Finns (green) and Estonians (blue) as a function of the deviant stimulus, arranged in the order of increasing F2 difference from the standard stimulus. Bars indicate SEM. (ii) MMN (at frontal, Fz) (unbroken lines) and MMNm (left hemisphere) (broken line) peak latencies as a function of the deviant stimulus for Finns (green) and Estonians (blue). (iii) Strength of the equivalent current dipole (ECD; average of nine Finnish subjects) modeling the left auditory cortex MMNm for the different deviant stimuli. (iv) Left- and right-hemisphere MMNm of one typical Finnish subject for deviants /ö/ (top, prototype) and /õ/ (bottom, non-prototype) presented in contour (spacing 2fT cm⁻¹) maps of the magnetic field gradient amplitude at the MMNm peak latency. The squares indicate the arrangement of the magnetic sensors. The arrows represent ECDs that indicate activity in the auditory cortex; the black dots in these arrows show the centers of gravity of MMNm. Note that the /ö/ phoneme elicits a much larger MMNm in the left than right hemisphere, whereas the responses to /õ/ (non-phoneme to the subject) in both hemispheres are small and quite similar in amplitude. Adapted, with permission, from Ref. 27.

manifestations of primitive sensory level intelligence, such as anticipation of next stimuli, speech sound perception (irrespective of the wide acoustical variation), and even simple concept formation, by recording MMN or MMNm. (This predominantly auditory cortex locus is supported by the results of related positron emission tomography[16] and functional magnetic resonance imaging[32,33] studies mentioned above.) Although we cannot definitely rule out the participation of suprasensory processes in the neural network involved, the role of the auditory cortex nevertheless seems to be predominant in carrying out these cognitive operations that go much beyond the role traditionally given to it as the highest end station of auditory perception. Consequently, it appears that the electrophysiological data reviewed represent a major step towards making the 'black box' of the cognitive operations of the human brain, as far as central auditory processing is concerned, somewhat more transparent, so that we now are able, probably for the first time, to monitor the occurrence of these higher order processes on-line and phase-by-phase as they occur in the brain.

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