PRE-ATTENTIVE PROCESSING OF COMPLEX AUDITORY INFORMATION IN THE HUMAN BRAIN

Doctoral Dissertation

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ABSTRACT

The present thesis aimed to illuminate the neurophysiological basis of pre-attentive memory functions involved in processing of complex auditory information. To this end, 10 studies were conducted in which electric and magnetic brain activity, time-locked to spectrally and/or temporally complex auditory stimulation, was recorded from healthy adults. During the recordings, the subjects concentrated on reading and ignored the auditory stimulation.

The present data indicated that remarkably complex auditory stimulus information is pre-attentively encoded by cortical memory traces. Interindividual differences in these pre-attentive brain functions were associated with differences in interindividual perceptual and cognitive abilities in sound processing. In addition, a part of the auditory cortex was found to be specialized in encoding changes in tone frequency when presented among complex stimuli. In sum, the present results emphasize the importance of pre-attentive processes in encoding spectrally and temporally complex auditory stimuli.

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VANHEMMILLENI
VIENOLLE JA AARNELLE

Preface

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LIST OF PUBLICATIONS

The present thesis is based on the following studies (referred to in the text by their Roman numerals):

I Tervaniemi, M., Saarinen, J., Paavilainen, P., Danilova, N., Näätänen, R. (1994) Temporal integration of auditory information in sensory memory as revealed by the mismatch negativity. *Biological Psychology*, **38**, 157–167.

II Tervaniemi, M., Maury, S., Näätänen, R. (1994) Neural representations of abstract stimulus features in the human brain as reflected by the mismatch negativity. *NeuroReport*, **5**, 844–846.

III Yabe, H., Tervaniemi, M., Reinikainen, K., Näätänen, R. (in press) Temporal window of integration revealed by MMN to sound omission. *NeuroReport.*

IV Tervaniemi, M., Schröger, E., Näätänen, R. (1997) Pre-attentive processing of spectrally complex sounds with asynchronous onsets: an event-related potential study in human subjects. *Neuroscience Letters,* **227**, 197–200.

V Winkler, I., Tervaniemi, M., Huotilainen, M., Ilmoniemi, R., Ahonen, A., Salonen, O., Standertskjöld–Nordenstam, C.–G., Näätänen, R. (1995) From objective to subjective: pitch representation in the human auditory cortex. *NeuroReport*, **6**, 2317–2320.

VI Ross, J., Tervaniemi, M., Näätänen, R. (1996) Neural mechanism of the octave illusion: electrophysiological evidence for central origin. *NeuroReport,* **8**, 303–306.

VII Näätänen, R., Schröger, E., Karakas, S., Tervaniemi, M., Paavilainen, P. (1993) Development of neural representations for complex sound patterns in the human brain. *NeuroReport*, **4**, 503–506.

VIII Tervaniemi, M., Alho, K., Paavilainen, P., Sams, M., Näätänen, R. (1993) Absolute pitch and event–related brain potentials. *Music Perception*, **10**, 305–316.

IX Tervaniemi, M., Ilvonen, T., Karma, K., Alho, K., Näätänen, R. (1997) The musical brain: brain waves reveal the neurophysiological basis of musicality in human subjects. *Neuroscience Letters,* **226**, 1–4.

X Alho, K., Tervaniemi, M., Huotilainen, M., Lavikainen, J., Tiitinen, H., Ilmoniemi, R.J., Knuutila, J., Näätänen, R. (1996) Processing of complex sounds in the human auditory cortex as revealed by magnetic brain responses. *Psychophysiology*, **33**, 369–375.

Abbreviations and Terminology

μV	microvolt, unit for the strength of the voltage change in EEG recordings
AP	absolute pitch; ability to name a tone after its name in musical scale or to produce a tone of desired pitch without a reference tone
Chord	A combination of tones which belong to the same musical scale in Western music (selection of 7 tones from 12 possible tones within an octave). The presentation of the tone can be either parallel or sequential.
ECD	equivalent current dipole; models (in the least square sense) optimally the recorded MEG signal
EEG	electroencephalogram: brain electric activity which is mainly caused by the excitatory post-synaptic potentials in the fourth cortical layer
ERP	event-related potentials; received after averaging across several tens or hundreds of EEG epochs following a stimulus presentation
fT/cm	femtotesla/cm; unit for the magnetic field gradient in MEG recordings
Fundamental	The lowest harmonic partial present in a spectrally rich tone. If the fundamental frequency is missing the perceived pitch is not changed.
ISI	Inter-stimulus interval; denotes the silent period from the offset of a stimulus until the onset of the following stimulus.
MEG	Magnetoencephalogram; records the magnetic field outside the head created by electric brain activity
MMN	Mismatch negativity; an ERP component which reflects the discrepancy between neural trace and incoming sensory input.
MMNm	the magnetic counterpart of MMN
N1	A negative ERP wave with several subcomponents which peaks appr. 100 ms after stimulus onset; one subcomponent reflects the activation of frequency specific neurons.
N1m	the magnetic counterpart of electric N1
N2b	A negative ERP component which overlaps or follows the MMN in active experimental paradigms, also in passive paradigms if an easy primary task and wide stimulus deviance is employed.
Partial	One frequency component present in spectrally rich tones, produced, e.g., by musical instruments.
Pure tone	=> sinusoidal tone
Sinusoidal tone	Tone, caused by an oscillator, which has only one partial (frequency component).
SOA	Stimulus onset asyncrony; used to indicate the asynchrony between successive stimulus onset or the asynchrony of successive stimulus part onsets.

1 PRELUDE ON AUDITORY PERCEPTION

Since the days of Pythagoras, scientists have been interested in the psychological and physiological mechanisms of auditory perception. The earliest related experimental attempts were made by Seebeck (1841) and Helmholtz (1877/1954) who significantly contributed to the understanding of pitch perception. Despite subsequent theoretical as well as experimental achievements in perceptual and cognitive psychology of audition (Deutsch, 1982; Dowling & Harwood, 1986; Krumhansl, 1990; McAdams & Bigand, 1993; Moore, 1989), the neural basis of auditory perception, especially when complex non-verbal auditory information is involved, has remained relatively unknown. Only during the last two decades, due to parallel development of brain-imaging techniques and computer-controlled sound-production possibilities combined with theoretical work, fast progress has taken place in the study of the neural basis of auditory perception.

In the following, an overview on auditory perception and its neural basis will be given in Chapter 1. Thereafter, recent electroencephalographic (EEG) and magnetoencephalographic (MEG) results, received by recording brain activity related to auditory processing, will be introduced and discussed in Chapters 2-6. These chapters are organized according to the topics investigated in Studies I–X which form the present thesis. The conclusions will be summarized and discussed in Chapter 7.

1.1 From air-pressure changes to sound perception

Sound perception is based on air-pressure changes initiated by a sound source (e.g., a played musical instrument or a speaker). In its simplest case, a sound consists of only one frequency of one static amplitude, i.e., it is a pure sinusoidal tone produced by an oscillator. In a more complex case, as with speech, music, and environmental sounds, sound consists of several simultaneous frequencies. The sound spectrum depends on the sound source. It also varies as a function of time and the sound frequency e.g., within a scale played by a given instrument (Sundberg, 1991).

The air-pressure changes are encoded as a sound by a sequence of neural events (for an overview, see Buser & Imberty, 1992). These events originate in the cochlea of the inner ear, where hair cells of the organ of Corti above the basilar membrane are activated. The cells are tonotopically organized, that is, they are positioned according to the tone frequency to which they maximally respond (Pickles, 1988). The hair cells consequently activate auditory nerve fibres which transmit the neural impulses to the brain stem, middle brain, and thalamic nuclei (Figure 1A). These nuclei, preserving the tonotopy, mainly contribute to sound localization (Masterton, 1992) and

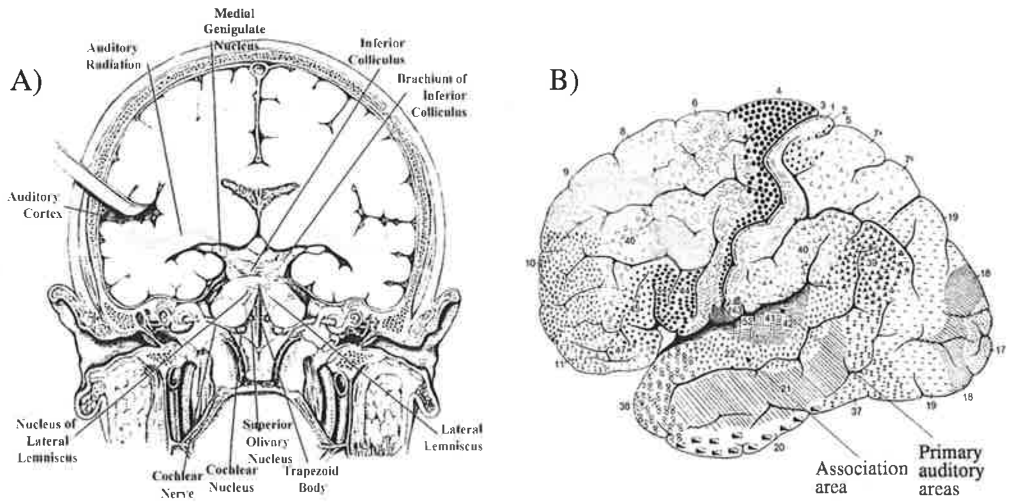


Figure 1A. A schematic illustration of the ascending auditory pathways and nuclei involved auditory processing. The head is here viewed from the back. Note that the pathways mainly lead to the hemisphere contralateral to the stimulated ear. For the sake of clarity, the descending auditory pathways are not presented here.

B. A lateral view from the left side to the human cortex. The primary auditory areas are marked by numbers 41 and 42 and the auditory association areas by number 22 (the numbering corresponding to the classical Brodmann classification).

to periodicity analysis conducted when a sound consists of multiple harmonic components (Langner, 1992). From the thalamus, the neural tracts lead the activation to the auditory cortices contralateral and ipsilateral to the stimulated ear (Pickles, 1988). These connections facilitate further the sound localization since in both cortices, neuronal populations exist which are selectively activated by sounds presented in either ipsilateral or contralateral side (Phillips and Brugge 1985, see also Connolly, 1993). From the auditory cortex, there are cortico-cortical connections to the opposite hemisphere (called corpus callosum) and also descending neural tracts to the cochlea (Pickles, 1988).

The cortical areas mainly devoted to auditory processing are located in the vicinity of the Sylvian fissure in the left and right temporal lobes (FIGURE 1B). Animal studies have indicated that the majority of the neurons in the primary auditory cortex respond to auditory stimulation, either to all tones or only to complex sounds, e.g., to species-specific vocalizations (Evans, 1992; Pickles, 1988; Suga, 1992). In humans, by stimulating the temporal lobe electrically during surgery for the treatment of epilepsy, auditory perceptions of different types were caused to the patient, depending on the stimulated area (Penfield & Perot, 1963). Stimulation directed to the primary auditory cortex led to elementary tone perceptions, whereas stimulation to the associative areas caused more holistic perceptions, e.g., of sentences or melody fragments. More recent neuropsychological studies with brain-lesioned patients (e.g., Aaltonen et al., 1987; Tramo et al., 1993) confirmed this finding. Moreover, the auditory cortices have areas where the neurons are spatially organized according to the tone frequency (tonotopical organization; Romani et al., 1982; Tiitinen et al., 1993; Wessinger et al., 1997; see also Buser & Imberty, 1992) or intensity (Heil et al., 1994) to which they maximally respond.

The two hemispheres are specialized in processing auditory information differentially so that the left hemisphere is more involved in processing linguistic information and the right hemisphere in processing non-linguistic information (see, for example, Critchley & Henson, 1978). The right auditory cortex dominates in processing spectrally or temporally complex non-verbal information and also in perceiving non-verbal aspects of speech, e.g., its prosody and emotional content. These conclusions about hemispheric asymmetry in auditory perception were originally derived from clinical evidence following lesions in the right vs. left hemispheres (for reviews, see Damásio & Damásio, 1978; Marin, 1982) and from dichotic-listening studies, the method introduced by Kimura (1964) (Bever & Chiarello, 1974; Messerli et al., 1995; Paquette et al., 1996). Due to methodological limitations, however, conclusions concerning neural functions of the intact human brain which rely on these data only should be viewed with caution. First, lesioned cells may have had important connections to further processing loci and thus their malfunction impairs later (e.g., attentional) processing stages rather than the basic sensory processes. Second, the results of dichotic-listening studies are very sensitive to changes in experimental setup as well as to variation in the degree of subjects' formal training in music.

However, by utilizing modern brain-imaging techniques, this right-hemispheric dominance in attentive processing of non-verbal auditory information has recently been confirmed. For instance, it was found that monaural verbal stimulation activated the left hemisphere areas whereas monaural chords activated more the right hemisphere, specifically, the frontotemporal areas (Mazziotta et al., 1982). It was also shown that the left hemisphere was activated in a pure phonetic decision task whereas the right hemisphere areas were more active when the pitch contour of that verbal material was to be determined (Zatorre et al., 1992; see also Auzou et al., 1995; Zatorre et al., 1994).

1.2 Auditory information processing

The processing of auditory information have traditionally been schematized as follows. Physical features of auditory information are represented by the pre-attentive sensory (echoic) memory (Neisser, 1967) including two phases: The shorter with a duration of 150-350 ms and the longer up to 10-20 seconds (Cowan, 1995). The relevant parts of auditory information are further processed in the working memory under attentive control (Baddeley, 1986; Cowan, 1995; Näätänen, 1992). The long-term memory representations help in interpreting the on-going flow of auditory information. They are also simultaneously updated by the new input (Neisser, 1967). The functioning of these looped and partially overlapping phases forms the basis for our auditory perceptions. Although this memory model was mainly developed on the basis of verbal material, it does not need essential modifications to cover non-verbal auditory information processing as well, especially with regard to the working and long-term memory phases. For instance, in recognition of an instrumental melody with accompaniment, the successive tones are kept in working memory while their internal relations are analyzed (e.g., the tones belonging to the same melodic line are grouped on the basis of their pitch or timbre) (McAdams, 1993). The melody is then matched with the long-term melody lexicon either with verbal information (the melody title, the lyrics) or merely with non-verbal parts of it (the melodic contour and rhythm) (McAdams, 1993). The long-term representations of the dominant musical culture continuously guide our listening. The listener immediately detects the tones which are discrepant with the implicitly learned regularities of music and thus with expectations formed about its continuation (Krumhansl, 1990; Jones, 1981, 1982).

However, the role of pre-attentive processes in perceiving spectrally and temporally complex, e.g., musical information, has remained relatively unclear. For that, two reasons might be suggested. First, sensory memory was traditionally regarded as a pre-attentive 'storage' of stable features of the auditory environment (Broadbent, 1958; for more elaborated views, see, however, Massaro, 1975), whereas in music perception, the importance of expectations for the incoming information was generally emphasized. Second, even after the new brain research paradigms for investigating the pre-attentive memory functions were introduced in late 1970's, subsequent experiments used mainly pure sinusoidal tones of short duration to ensure a proper experimental control, leaving us without experimental evidence about brain processes related to more complex stimulation. During the last decade, however, the first assumption has been explicitly questioned from theoretical grounds (Näätänen, 1992). Simultaneously, the improved computer-controlled sound-producing techniques have enabled the creation of well-controlled complex stimuli that have allowed one to better determine the accuracy and limits of sensory memory in encoding complex auditory information as well.

1.3 The pre-attentive neural processing of auditory stimuli

The neural mechanisms of auditory processing, including pre-attentive processes, can be investigated by recording electric brain activity (electroencephalogram, EEG) above human scalp. By averaging several EEG epochs following the presentation of a stimulus under interest, the electric activity related to its neural processing can be revealed with a millisecond accuracy (Picton et al., 1983; Johnson & Baron, 1995). After applying averaging procedure, several ERP deflections (waves) can observed. The earliest of them occur only 1-10 ms after a stimulus presentation. These responses are generated in brainstem and labelled after their temporal order (I - VII) (Picton, 1980). Subsequent middle-latency responses which can be observed 15–40 ms after stimulus onset are generated in the auditory cortex (e.g., Celesia, 1976). They are labelled after their polarity and temporal order (N0, P0, Na, Pa, Nb). Like later P1, N1, P2, and N2 waves with peak latencies between 50 and 200 ms, these early deflections are mainly determined by the stimulus features whereas some other late ERP deflections reflect memory- and attention-related stimulus processing (Näätänen, 1992). These late deflections and components are referred to by their polarity and latency or by their specific function (Johnson & Baron, 1995). For instance, P300 wave is a positive wave peaking around 300 ms (Donchin, 1981) and mismatch negativity (Näätänen et al., 1978) is a negative component reflecting a mismatch between neural memory representation and new sensory information (see below).

An ERP component called *mismatch negativity* (MMN) is evoked by an infrequently presented stimulus ("deviant"), differing from the frequently-occurring stimuli ("standard") in one or several physical parameters like duration, intensity, or frequency (Näätänen, 1992). The MMN is not elicited by stimuli with deviant stimulus parameters when they are presented without the intervening standards. The MMN has, therefore, been suggested to reflect a change detection when a pre-attentively formed memory trace representing the constant standard stimulus and the neural code of the stimulus with deviant parameter(s) are discrepant (Näätänen 1990, 1992). For illustration of typical ERPs for standard and deviant tones, see FIGURE 2.

MMN is generated automatically in the sense that it is elicited even during the performance of a simultaneous task unrelated to auditory stimuli like reading a book or playing a computer game (Alho et al., 1992; STUDIES I–X). Although the MMN amplitude may be enhanced by directing attention to the auditory stimuli (Alain et al., in press; Oades & Dittmann-Balcar, 1995) the evidence for its automatic generation (even with remarkably complex auditory information when binaural stimulation is used; see Paavilainen et al., 1995) and its close relation to subsequent attentive performance (see below) advocates its usefulness as an objective task-unrelated measure of the accuracy of the human brain in encoding auditory information (Näätänen, 1995).

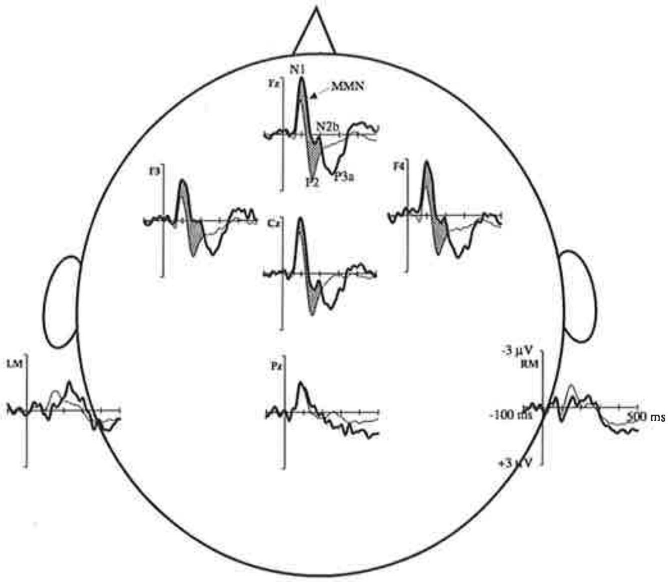


Figure 2. The auditory event-related potential (ERP) curve recorded at seven electrode positions. Each ERP curve illustrates an average across 8 subjects. The thin line denotes an ERP to a frequently presented standard tone of 600 Hz. The thick line denotes an ERP to an infrequently presented deviant tone of 660 Hz. The stimuli were sinusoidal tones, 100 ms in duration,and they were presented once per second. Successive ERP deflections are named according to their polarity and peak latency. The MMN and N2b components are denoted by shading. (Data adapted from Kujala et al., 1997).

The MMN elicitation by a deviant stimulus is prevented if the stimulus onset asynchrony (SOA; determining the time difference between adjacent stimulus onsets) is prolonged over 10 seconds (Sams et al., 1993). This provides us with an approximation for the decay time of the pre-attentive memory trace which corresponds to some estimations for the duration of the longer phase of sensory memory as obtained with behavioral methods (Cowan, 1995). However, it seems that after a permanent memory trace has been established it may be refreshed, even after a break over 10 seconds, by a single standard stimulus presentation (Cowan et al., 1993; see also Winkler et al., 1996). In contrast, if no stable memory representation for the standard tone has been established, several standard stimulus presentations are needed to form a trace.

Several different brain research methods have revealed that the MMN is generated mainly in the auditory cortex or in its immediate vicinity (for a review, see Alho, 1995). The auditory-cortex origin of MMN has been shown by magnetic (MEG; e.g., Hari et al., 1984; Tiitinen et al., 1993) and intracranial recordings (Halgren et al., 1995; Kropotov et al., 1995). In electric recordings, this is reflected by the polarity reversal of the MMN above the Sylvian fissure from a negative maximum recorded above the fronto-central regions to a positivity at the mastoids (when a nose reference is used) (e.g., Alho et al., 1986; Paavilainen et al., 1993). Additional generators have been found in the frontal (Giard et al., 1990) and parietal (Levänen et al., 1996) lobes.

Through several experiments employing sinusoidal tones, the functions of pre-attentive brain mechanisms have been established for several sound parameters, including (among others) stimulus frequency, duration, intensity, and locus of origin (for reviews, see Näätänen, 1992, 1995). Moreover, the first MMN results showed that the magnitude of physical deviation between the standard and deviant stimuli is reflected by MMN amplitude and latency: for instance, a MMN to a frequency change was larger and earlier for larger frequency deviances (Sams et al., 1985). However, even more interesting were the results showing that MMN reflects the perceptual accuracy as determined by the Seashore musicality test (Lang et al., 1990; for the Seashore test, see Seatveit et al., 1940) and by behavioral discrimination tasks employing the same stimuli than MMN recordings (Tiitinen et al., 1994). This correlation between MMN elicitation and perceptual abilities implies that attentive performance is based on the accuracy and efficiency of the pre-attentive neural mechanisms.

1.4 The aim of the present study

The present thesis illuminated the pre-attentive neuronal processing of complex auditory information. As reviewed above, the majority of our present knowledge about auditory processing has been achieved by research employing sinusoidal sounds. However, these studies left several questions unanswered. What are the limits and accuracy of the pre-attentive brain functions which are relevant in natural acoustic environment? Are the previous theories in cognitive psychology valid with regard to auditory information processing with complex stimulation? Can the neural basis for interindividual differences in learning to discriminate between natural sounds (essential, e.g., while learning a new language) be revealed at the pre-attentive level? Can auditory illusions be explained by pre-attentive neuronal mechanisms?

To this end, 10 studies were conducted in which the complexity of the auditory stimulation was systematically varied and the electric brain activity related to the processing of these sounds was recorded. These data will be introduced and discussed in the following chapters. First, data revealing that the pre-attentive mechanisms encode complex stimuli and even abstract relations between them will be reviewed. Second, it will be discussed whether the illusory auditory perceptions can be explained by pre-attentive functions. Third, it will be shown how learning or special skills like musicality is indexed by MMN. Fourth, it will be suggested that the auditory-cortex areas involved in pre-attentive auditory processing are functionally specialized. General methods related to data recording and analysis of the studies forming the present thesis are presented in Appendix.

2 PRE-ATTENTIVE PROCESSING OF COMPLEX SOUNDS

As reviewed above, the first experiments investigating pre-attentive auditory functions were conducted with single sinusoidal tones. The experiments to be introduced in the following were conducted to determine whether auditory stimulation with more complex temporal or spectral features could also be encoded pre-attentively.

2.1 Paired tones

Study I of the present thesis aimed at determining whether information of the temporal order of two successive stimuli is represented by pre-attentively formed neural traces. This was done by determining the presence of the MMN to the changed order of tone pair members differing in frequency. All standard pairs had an ascending frequency change (labelled schematically as "a-b", "a" being lower in frequency than "b"). These pairs were occasionally replaced by deviant pairs in which the tones were presented in either descending (reversed) order (b-a), were of a same frequency (a-a, b-b), or the second tone was omitted (a-) (Figure 3).

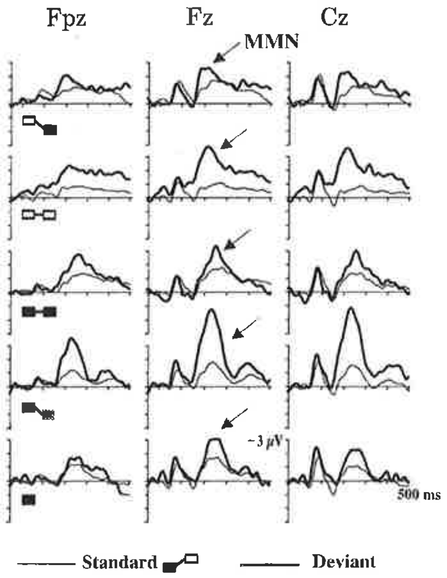


Figure 3. ERPs recorded to tone pairs from reading subjects (N=10). The stimuli were sinusoidal paired tones which were presented to the subjects' left ear via headphones. In all conditions, the standard tone pair consisted of an ascending frequency change within the pair, the lower tone being 658 Hz (illustrated by a black square; sinusoidal tone of 60 ms; corresponding to E^5 in the Western musical scale) and the higher tone 739 Hz (illustrated by a white square; sinusoidal tone of 60 ms; corresponding to Fsharp^5). The successive tones, forming a pair, were separated by a 40 ms silent inter-stimulus interval and the successive tone pairs by 640 ms.

The experiment consisted of five conditions. The deviant tone pair consisted either of (1) reversed frequencies (causing a descending tone pair; first row), (2) replacement of the first tone with the second frequency (second row), (3) the repetition of the first frequency (third row), (4) a third, lower frequency as its second member, causing also a descending tone pair like in the first row but with a new lower frequency element (fourth row), or (5) an omission of the second tone (fifth row).

The frequencies and timing of the deviant tones pairs is indicated below the ERP curves. The MMN is indicated by the arrows. (Data from Study I.)

It was found that all these changes in the within-pair sound order elicited the MMN, indicating that the tone frequencies and their temporal order were pre-attentively encoded. The MMN latency was longest in the condition in which the first tone was replaced by the frequency of the second tone (after the different onset-time of the deviant tone in different conditions was taken into account in the latency analysis) (Figure 3: the second row). Its amplitude was largest when the deviant tone pair included a new frequency (Figure 3: the second row from bottom). These latency and amplitude data indicate that while the deviant pair with the new frequency deviated most from the neural trace formed for the standard pair, the deviant pair in which the first tone frequency matched to the frequency of the second tone, deviated least. Since the MMN was elicited even by the omission of the second member of a pair it was concluded that the standard pair was encoded as one combined stimulus entity, consisting of a conjunction of two tones rather than two successive single tones (see also Section 3).

In addition to their frequency content, it was recently shown that tone pairs can be temporally structured pre-attentively on the basis of their intensity relations (Schröger et al., 1995). In this study, standard stimulation consisted of tone pairs with tones differing in intensity (70–58 dB SPL). The deviant tone pairs with a reversed intensity relation (58–70 dB SPL) elicited an MMN.

Saarinen et al. (1992) have also shown that if the stimulus pairs vary in their absolute frequency level, the deviant pairs still elicit the MMN. Their standard feature was an ascending frequency change presented randomly at several absolute frequency levels (like '...a-b, c-d, b-c, d-e...'). An MMN was elicited by deviants with reversed descending change (like '...b-a, c-b, d-c...'). The result thus shows that even primitive concepts ('rise', 'fall') may be pre-attentively formed.

A complementary approach was adopted by Hari et al. (1992). They compared the strength of frequency MMNm (denoting the magnetic counterpart of the electric MMN) elicited by single sinusoidal tones ('...a, a, a, b...') with the same frequency change included in a tone pair ('...a-a, a-a, a-a, a-b...'). In the latter case the MMNm was of larger amplitude. This led the authors to conclude that the memory trace for the standard (i.e., more frequently presented tone 'a') is stronger when paired stimulation was employed. Recently, however, Csépe et al. (1997) failed to replicate this result. One possible explanation, offered by Csépe et al., is that they employed rather a small frequency difference between the tones (1000-1050 Hz instead of 1000-1200 Hz as in Hari et al., 1992). Consequently, tones with smaller frequency separation may be more readily incorporated into a perceptual unit, whereas tones with larger frequency separation may be encoded as separate entities. It should be noted that in both studies, the deviant stimulus introduced a new frequency element not present in the standard stimulus. In such a case, a N1(m) wave, reflecting the activation of different set of frequency-specific neurons (Näätänen

& Picton, 1987), also contributes to the recorded response, overlapping the MMNm. Particularly this may have taken place when paired stimuli were employed, as the rate of rare-frequency tones per time unit was smaller than with single tone stimulation ('...a, a, a, b...' *vs.* '...a-a, a-a, a-a, a-b...'). This N1 contribution can be observed also in the STUDY 1 (FIGURE 1: second row from bottom). In addition, the larger frequency difference may have further enhanced the N1m wave in Hari et al.'s data.

In sum, the MMN data of the STUDY I and related studies indicate that temporal properties of short tone patterns and abstractions of their frequency content are pre-attentively encoded by the human brain. This suggests that even pre-attentively, auditory information is encoded as 'events' rather than as an unanalyzed tone series. Keeping in mind the importance of temporal cues in music (Jones & Yee, 1993) and speech (Rosen, 1992) perception, the present result opens promising ways for investigating the accuracy of the temporal processing at the pre-attentive level (see, e.g., Pihko et al., 1997).

2.2 Regularly spaced complex tones

Interestingly, regular features of auditory information seem to be encoded pre-attentively even when this information is not structured by silent intervals to temporally separate 'events' (like in paired stimulation as introduced above). For example, Nordby et al. (1988) presented a regularly alternating tone sequence ("...a-b-a-b-...") and showed that occasionally repeated tones ("...a-b-a-**a**... ") elicited the MMN. This suggests that the alternating frequencies were pre-attentively processed to form a 'rule' against which a repetition deviated.

In STUDY II, one further step was taken to determine whether an abstraction of frequency decrease within a continuous stimulus stream (and not merely that presented as isolated tone pairs as in Saarinen et al. (1992) discussed above) could be encoded pre-attentively. To create a strong expectation for a continuously decreasing pitch, the Shepard-tone illusion (Shepard, 1964) with a 12-tone sequence was utilized. Shepard tones (FIGURE 4A) are perceived as an endlessly ascending or descending sequence of sounds (depending on their presentation order), without a sense of their octave (exact pitch height) (FIGURE 4B). Within such a sound sequence with apparently continuously decreasing pitch, two types of deviant sounds were presented; one repeating the previous pitch (...'e-d-c-b-**b**-...') and another ascending in pitch (...'e-d-c-b-**c**-b-...') were delivered in separate blocks, to see whether these 'rule-deviating tones' elicit the MMN.

The results indicate that with Shepard tones, both repetitive and ascending sounds elicited an MMN (FIGURE 4C: left column). This result was replicated with sinusoidal tones with ascending deviants but not with repetition deviants with which the MMN did not quite reach statistical significance (FIGURE 4C: right column).

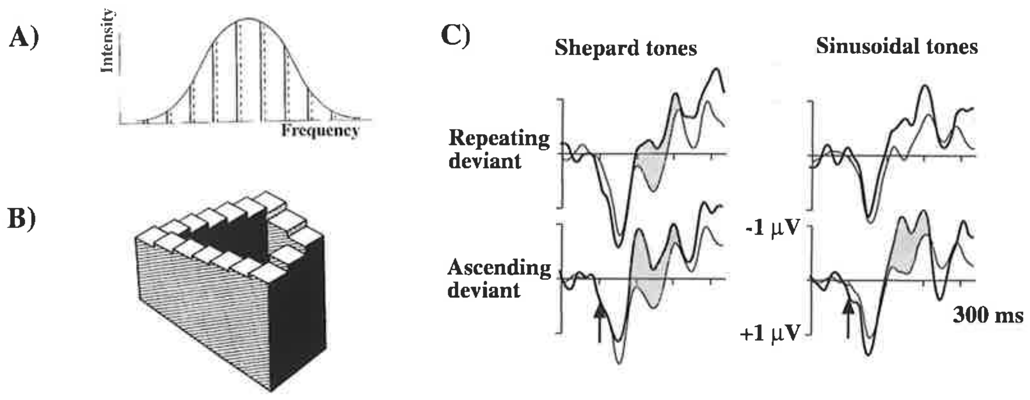


Figure 4A. A spectrum of an individual Shepard sound which, when presented in ascending/descending sequences of 12 sounds in one semitone steps, causes a pitch to ascend/descend in an endless manner. One Shepard sound consists of 10 frequency components, of one octave apart, with a bell-shaped spectrum. While a 12-tone series of Shepard sounds is delivered, the tone-height (= 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/descending stairs.

C. The ERPs recorded at Fz electrode from reading subjects (N=8) to Shepard and sinusoidal tones (thin line: standard stimulus, thick line: deviant stimulus; binaural stimulation). The left column: regularly descending Shepard sound sequence randomly replaced by repetitive (on the top) or ascending (on the bottom) deviants. The right column: regularly descending sinusoidal tone sequence replaced by repetitive (on the top) or ascending (on the bottom) deviants. The arrow indicates the onset of the stimulus and the shadowed area the MMN which was significant in statistical analysis. (Data from STUDY II.)

In general, the present result suggests that even at the level of pre-attentive processing, the regularity of auditory stimulation may be abstracted, despite the continuous change in physical stimulus material. Moreover, primitive expectations concerning the incoming auditory information may be created pre-attentively as indexed by MMN elicitation especially with Shepard tones with rich spectral structure in both experimental conditions. Since sinusoidal stimuli contain less spectral information it may be that larger physical stimulus changes in them are needed to MMN elicitation reflecting a pre-attentive deviance detection - MMN was elicited with ascending but not with repeating deviants when tones were sinusoidal (see also Sections 5.2 and 5.3).

Alain et al. (1994) studied further how the SOA and the frequency difference between successive stimuli affect the MMN amplitude for a 'rule-violating' deviant tone (e.g.,'... a-b-a-b-a-**a**...'). A MMN was larger when the tones were presented with short SOAs and separated by a large frequency difference than when either smaller frequency difference or a long SOA were used. The authors concluded that the shortened time interval between the successive stimuli and the larger magnitude of deviance enhanced the pre-attentive detection of rule violation.

Furthermore, recent evidence indicates that a 'rule' about the continuation of a sound sequence can also be based on intensity information, in addition to frequency information (Schröger et al., 1996). The authors employed regularly spaced sinusoidal tones of two intensities as a standard event. Deviant events of two kinds were presented: the repetition of the softer sound and the repetition of the louder sound. Both deviant events elicited the MMN.

In conclusion, the present MMN evidence indicates that the regular features of auditory information (despite the continuous change of the physical stimulus information) are encoded pre-attentively, at least when parameters structuring the sequence involve frequency or intensity. This indicates that primitive expectations concerning the characteristics of the next stimulus might even be pre-attentively formed.

3 TEMPORAL WINDOW OF INTEGRATION AS REFLECTED BY THE MMN

The shorter store of sensory memory has, according to the behavioral studies, a limited temporal span, estimates for its duration varying from 150 to 350 ms (for reviews, see Moore, 1989; Cowan, 1995). This period could also set limits on the temporal perceptual integration process that binds closely presented stimuli together (Näätänen, 1990, 1992). In three studies of the present thesis it was investigated whether this perceptual integration window is reflected in MMN elicitation. This was conducted by presenting successive stimuli or stimulus parts during and across the integration window. STUDIES I and III employed stimulus omission as the deviant event. STUDY IV employed spectrally complex tones with asynchronously starting frequency components. Thus it was wished to determine whether the same temporal constraints in MMN elicitation are valid with discrete (single, paired) and continuous stimulation.

3.1 Stimulus omissions in paired and in regularly spaced stimuli

STUDY I included a condition in which the temporal effects of stimulus omission as a function of the inter-pair interval to the MMN elicitation were investigated. The within-pair SOA was either 100, 200, 300, or 400 ms. It was hypothesized that if both tones fall within the temporal window of integration, the omission of the second tone would elicit the MMN.

The results showed that while an omission MMN was still elicited with SOAs of 100 (FIGURE 3, bottom row) and 200 ms (FIGURE 5A, top row), it was no longer present with SOAs of 300 and 400 ms (FIGURE 5A, middle and bottom rows). This result was considered to indicate that the tone pair was encoded as a unitary event by sensory memory when its duration was shorter than the integration window. In other words, a tone pair was not encoded as two separate stimuli but as an entity, omission of the second stimulus eliciting an MMN like in the case of shortened single stimulus.

To further test the temporal integration hypothesis, an experiment employing regular (that is, not paired) stimulus rate was conducted (STUDY III). Constant SOAs varied in separate blocks from 100 to 350 ms. According to these results, an omission MMN was elicited with SOAs 100 and 125 ms (STUDY III; FIGURE 5B). With longer SOAs no omission MMN was elicited.

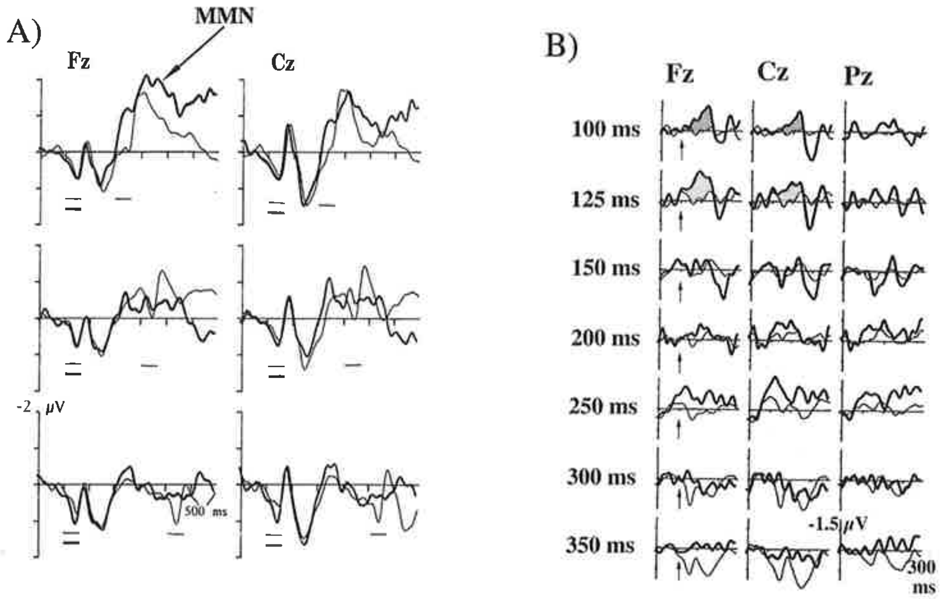


Figure 5A. ERPs recorded from reading subjects (N=13) to omissions of the second member of a tone pair with varied SOAs as indicated on the left. In the standard tone pair, there were two tones of different frequencies in ascending order (658 Hz and 739 Hz). Thin lines below the ERP curves indicates the timing of a standard tone pair. The thick line indicates the timing of deviant tones, without the second tone in a pair. The successive tones were separated by a 200 ms SOA (the topmost row) which was in different conditions prolonged by 100 ms steps until 400 ms. The stimuli were delivered to the subjects' left ear via headphones. The MMN is indicated by an arrow. (Data from Study I.)

B. ERPs recorded from reading subjects (N=9) to infrequently omitted stimuli (thick lines) and regularly spaced sinusoidal tones of 1000 Hz in frequency and 50 ms in duration (thin lines) (stimulation to the subjects' left ear via headphones). Seven different SOAs between 100 and 350 ms were employed, in separate conditions, as denoted on the left. The arrow indicates the timing of the omitted tone. The shadowed area indicates the omission MMN. (Data from Study III.)

The results from Studies I and III show that even a stimulus omission can elicit the pre-attentive MMN while previous experimental results did not display any clear-cut evidence regarding this issue (Näätänen et al., 1987; Joutsiniemi & Hari, 1989). In parallel, the present results also indicate that the stimulus omission does not necessarily evoke a pre-attentive brain response beyond the integration window. Moreover, the temporal limits for the integration window seem to equal those indicated by the shorter store of sensory memory (Cowan, 1995; Näätänen, 1992). However, they also show that the critical SOA optimal for temporal integration may differ between paired *vs.* continuous stimulation.

3.2 Temporal and spectral integration of complex sounds

To further investigate the temporal auditory information processing with more natural stimuli, Study IV employed temporally and spectrally complex stimuli (originally developed by Moore et al., 1985) (Figure 6 A). These stimuli consisted of 10 harmonic partials of 155-Hz fundamental frequency. In the deviant tones, the fourth partial was mistuned by ± 3% from its natural frequency, being 600 or 640 Hz instead of 620 Hz. As shown by Moore et al. (1985), if the mistuning is of relatively small magnitude, the mistuned harmonic partial is integrated with the remaining complex tone causing the complex-tone pitch to increase/decrease to the direction of the mistuning as a synthetic entity with one pitch. However, with larger mistunings (>3%), that partial is perceptually separated from the remaining complex tone. By employing such a stimulation it was investigated whether a very small frequency change in one of the harmonic partials might elicit the MMN. Moreover, Darwin & Ciocca (1992) showed that whereas the mistuned partials preceding the remaining complex tone by 160 ms or less is integrated to the complex-tone pitch, the mistuned partials with longer onset asynchronies are heard as separate entities. To determine whether the mistuned partial was pre-attentively integrated with the complex tone or not as a function of the onset asynchrony, this fourth partial (either tuned or mistuned) preceded the remaining complex tone, in separate blocks, by 0, 30, 90, 180, or 360 ms.

The MMN was elicited by a relatively small frequency shift (±3 %) in one of the 10 harmonic partials (Figure 6B). This indicates that in the case of harmonically rich tones, the changes in stimulus frequency are pre-attentively encoded very accurately. Moreover, the deviant-pitch tones activated both pre-attentive mechanism, as indexed by MMN elicitation (Näätänen 1992), and attentive mechanism, as indicated by N2b elicitation (N2b is an ERP component reflecting involuntary attention switch towards stimulus changes if an easy primary task like reading is combined with an apparent change in stimuli; see, e.g., Novak et al., 1990; Näätänen, 1992). However, the N2b component was only present when the most informative complex-tone part of the stimulus followed stimulus onset during the temporal window of integration. That is, with SOAs between the adjacent stimulus parts (leading partial and complex tone part) of 90 and 180 ms, the complex-tone part with a mistuned partial elicited an N2b. With the 0, 30, and 360 ms SOAs, the complex-tone part with a mistuned partial elicited merely an MMN.

This result of Study IV suggests that the central nervous system is sensitized to switch attentional focus towards a change in the acoustic environment when the critical information occurs during the temporal window of integration. This result is in line with recent results of Schröger (1996) who showed distraction effects to behavioral performance in an auditory detection task when task-irrelevant distracting stimulus and task-relevant stimulus were separated by 200 ms, but not when the separation was prolonged up to 560 ms.

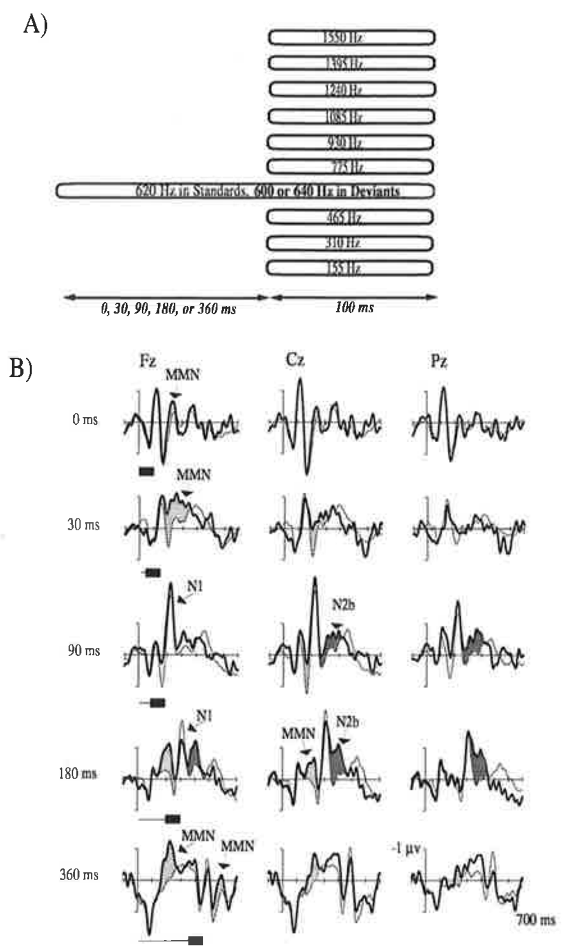


Figure 6A. A schematic illustration of the stimuli employed in Study IV. The alternative durations of the leading partial preceding the complex-tone part are marked on the left (bottom) and the frequencies employed in the harmonic complex are marked on the right. The duration of the leading partial corresponds to the term SOA.

B. ERPs recorded from reading subjects (N=10) during the presentation of stimuli differing in within-stimulus SOA as indicated on the left (binaural stimulation).

The thin line represents the standard-tone ERP (including 620-Hz partial; p=0.85), the thick line the deviant-tone ERP (ERPs to mistuned 600- or 640-Hz partials pooled together; p=0.075 for both). The light grey area represents the MMN. The dark grey area represents the N2b.

Stimulus onset is indicated under the Fz responses, and the amplitude and time scales are superimposed on the ERP in the right corner of the figure. (Data from Study IV.)

Taken together, the results of Studies I, III, and IV indicate the usefulness of MMN recordings in determining the duration of the shorter phase of sensory memory. Its duration seems to differ as a function of stimulus characteristics, that is, between paired and regularly presented sounds and also between sound omissions and other changes in temporal stimulus parameters. This suggests that even pre-attentive integration mechanisms, as indexed by MMN, are influenced by stimulus context.

4 ILLUSORY CODES AND ILLUSORY PERCEPTION

The studies discussed above dealt with cases when stimuli and the way in which they were perceived were congruent. Sometimes, however, our perceptions and the external reality do not correspond properly with each other. We may either derive more information than is actually provided by the stimulation or, alternatively, we may ignore part of the sensory information to be able to meaningfully interpret the sensory information as a whole. The Studies V–VI were conducted in order to determine the role of pre-attentive processing in these illusions.

4.1 Pre-attentive encoding of missing-fundamental pitch

An everyday example of a situation where listeners derive more information than actually carried by the physical signal is a telephone conversation. The speech signal normally contains frequency information between 100 and 5000 Hz, but the telephone transmits only frequencies between 300 and 3000 Hz. Despite the lack of fully adequate signal the speakers are able to follow each other. This phenomena has been broadly investigated in behavioral experiments where the lowest frequency component of a harmonically rich sound is omitted but the spectrally rich sound still results in a coherent perception, the perceived pitch corresponding to that of the missing partial. Consequently, the phenomenon is called the "missing fundamental" (MF; de Boer, 1976).

Study V aimed at finding out whether sensory memory could encode pitch information even with such vague physical information. This was done by recording the magnetic counterpart of MMN with a whole-head magnetometer to tones of a deviant missing fundamental pitch. The deviant was composed of 1200, 1800, and 2400 Hz components, creating an illusion of a 600-Hz missing-fundamental pitch. It was randomly presented among 9 different missing-fundamental sounds which all produced a standard 300-Hz pitch, despite their different spectral compositions and slightly different timbres (the standards were formed by three quasirandomly selected partials from the following frequencies: 900, 1200, 1500, 1800, 2100, 2400 Hz).

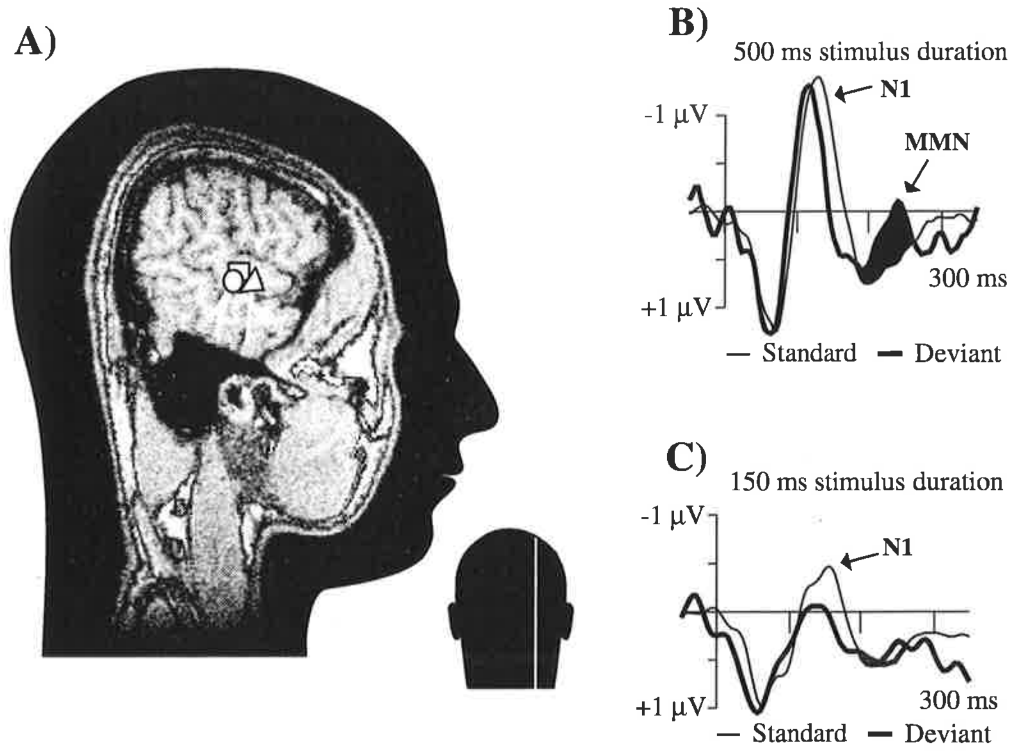


Figure 7A. The MMNm source (white circle) of a representative subject activated by a deviant 600-Hz missing-fundamental pitch presented among standard 300-Hz pitch sounds. The source was modelled by equivalent current dipoles (ECDs) and superimposed on a structural magnetic resonance image (MRI). The ECD produces optimally, in the least-squares sense, the recorded MEG signal, providing information about the spatial location, strength, and the orientation of the source. The square and triangle denote the N1m generator loci for standard and deviant pitch tones, respectively. (Data from Study V.)

B. ERPs recorded from reading subjects (N=12) elicited by missing-fundamental tones of 500 ms in duration which were presented to the subjects' right ear (thin line: standard 300-Hz tones; thick line: deviant 600-Hz tones). The MMN is indicated by the dark shadowing. (Data from Winkler et al., in press.)

C. ERPs recorded from reading subjects (N=10) elicited by missing-fundamental tones of 150 ms duration (thin line: standard 300-Hz tones; thick line: deviant 600-Hz tones). (Data from Winkler et al., in press.)

The results indicated that pitch-deviant MF tones elicited an MMN originating from the auditory cortex (Study V; Figure 7A). However, this took place in electric recordings only if the stimulus duration was 500 ms; with a 150 ms duration the MMN was absent (Winkler et al., in press; Figure 7B *vs.* Figure 7C). This suggests that with highly complex stimulation, long stimulus excerpts are necessary to pre-attentive encoding of the constant feature. Interestingly, N1 differed between the deviant and standard pitch tones with both stimulus durations. Behavioral data, indicating reliable pitch discrimination with 500 ms duration only, confirmed that attentional processes rely on neural encoding reflected by MMN rather than by N1.

4.2 Octave illusion

The opposite case of how stimulation and perception can be discrepant was studied with the octave illusion. In this illusion, binaural stimulation with two simultaneously presented frequency components of exactly one octave apart, is experienced not as two simultaneous stimulus streams but rather as a stimulus stream of single low and high frequencies alternating between the ears (Figure 8A; Deutsch, 1988).

Study VI aimed at determining whether this illusion is created pre-attentively. To this end, two kinds of deviants were delivered among illusion-creating standard stimulation (Figure 8A): In the first case, the deviant was consistent with the illusion (Figure 8B: top row). In the second case, the deviant was opposite to the illusion (Figure 8B: bottom row). By comparing MMN between these perceptually different deviant stimuli we wished to determine whether MMN to the illusion-consistent deviant is smaller or even missing, suggesting that the illusion-consistent deviant was encoded as resembling the perceptual image of the standard stimulation. Consequently, only the subjects perceiving the given stimulation in the illusory way were included in the ERP study.

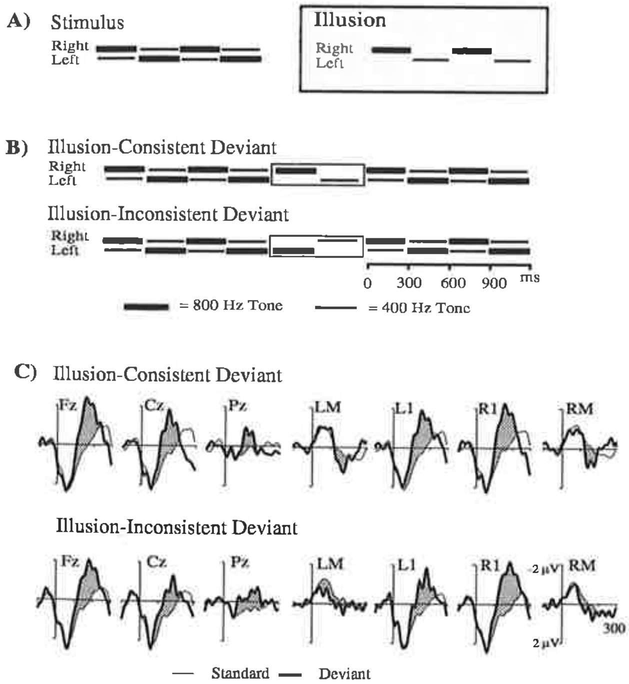


Figure 8 A. The standard event was a pair of successive dichotic sounds, each consisting of two simultaneous pure tones: 400 Hz (thin line) and 800 Hz (thick line). In the first pair, the high tone was presented to the right ear and the low tone to the left ear. In the second pair, the ears of presentation were reversed. This sound sequence is usually perceived by right-handed subjects as a string of alternating single high right-ear and low left-ear tones.

B. Illusion-Consistent deviant event was a pair of successive single pure tones, with the high tone (800 Hz) being presented to the right ear and the low tone (400 Hz) to the left ear. Illusion-Inconsistent deviant event consisted of the high tone presented to the left ear and the low tone to the right ear.

C. ERPs to standard (thin line) and deviant (thick line) stimuli with Illusion-Consistent (upper panel) and Illusion-Inconsistent (lower panel) deviants. The ERPs were recorded from reading subjects (total N=18). To MMN analysis were selected the subjects who in a post-experimental interview described the stimulation according to the octave illusion (N=9). The shadowing denotes the MMN. (Data from Study VI.)

The ERP data indicated that the MMN amplitude did not differ between the illusion-consistent and illusion-inconsistent deviant events, however (Figure 8C). This suggests that pre-attentive processes do not differ between stimuli which, during attentive listening, either provoke an illusory perception or not. In other words, pre-attentive mechanisms are not sufficient for encoding this binaural illusion but rather rely on physical stimulus parameters. This may partially result from the notable physical deviance employed in the present stimulation: omission of another tone from dichotic stimulation reduces the general intensity level of the stimulation which, in previous studies, has been shown to elicit a MMN (Nordby et al., 1994). In sum, it might be concluded that in the case of binaural octave illusion the illusory perception cannot be 'served' to the auditory system, instead, it needs to create that itself during attentive processing.

5 PRE-ATTENTIVE vs. ATTENTIVE PERCEPTION OF COMPLEX TONES

As reviewed above in Section 1.3, the pre-attentive processes govern the attentive processes in the case of sinusoidal tone perception with subjects unselected with regard to their musical abilities (Tiitinen et al., 1994) and also with subjects with divergent frequency-discrimination accuracy as shown in the Seashore musicality test (Lang et al., 1990). The following studies were conducted to determine whether similar correspondences between pre-attentive and attentive functions exist with more complex stimulus material.

5.1 Learning to discriminate unknown auditory patterns

In Study VII, subjects were presented with complex tone patterns (originally developed by Spiegel & Watson, 1981; their application for MMN studies being suggested by Port, 1991). These subjects were unselected with regard to their musical education and skills. The patterns consisted of 8 different frequencies, each of 50-ms duration, presented serially (Study VII; Figure 9). In deviant patterns, one of the frequency elements was replaced by an element of a higher frequency (650 Hz instead of 565 Hz). After each of the three ERP recording sessions with a reading task (each lasting about 30 minutes), the subjects' ability to detect deviant stimulus patterns was tested. During the test, their task was to press a reaction key after detecting a different pattern.

For those subjects who could immediately detect the deviants in the first discrimination test (hit rates in the three successive tests: 93, 91, and 88%), an MMN was elicited during the first ERP session. During the further sessions, their MMN latency significantly shortened. For those subjects who gradually improved their test performance during the experiment, the MMN was elicited only during the second and third sessions (hit rates: 39, 58, and 70%) (Figure 9). The present result indicates that the close correspondence between pre-attentive and attentive processes in auditory modality as previously shown with frequency changes presented among single sinusoidal tones (Lang et al., 1990; Tiitinen et al., 1994) exists also with more complex stimulus material.

Interestingly, in a control experiment without intervening discrimination conditions, the MMN was recorded as a small slow negative displacement during the first experimental phase but its amplitude remained unchanged during the subsequent ERP recordings (mean hit rate for these 14 subjects in the end of the experiment: 42%). This implies that for the learning to take place in the auditory modality, active listening seems to be of essential importance.

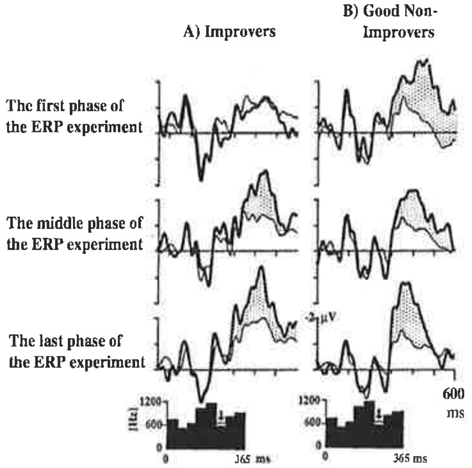


Figure 9. ERPs recorded at Cz electrode during reading to standard (thin line) and deviant (thick line) stimulus patterns (their timing and frequency content being illustrated below the ERPs; binaural stimulation). Left column: Data from subjects (N=7) who improved gradually during the experiment their performance in the discrimination task. Right column: Data from subjects (N=5) who could discriminate standard and deviant tone patterns already after the first (passive) stimulus blocks. (The data from Study VII.)

In sum, these results show that subjective discrimination accuracy in active conditions was paralleled by MMN elicitation during passive conditions. This suggests that neural mechanisms of certain long-term learning effects could also be reflected in MMN recordings (for complementary results recorded during attentive listening, see also Donald & Young (1982)). Moreover, active stimulus discrimination seemed to be of essential importance for the learning to take place, judging from the unchanged MMN amplitude in the control (reading only) experiment. However, as the main experiment indicates, the neural traces established during attentive listening can subsequently be activated even during a parallel reading task.

5.2 Musical subjects

The neural determinants for musical expertise have previously been searched for by several electrophysiological and anatomical studies. Of particular interest have been subjects with absolute pitch (AP) who can identify or produce a tone, for example, in terms of the Western musical scale without hearing a reference tone. In AP subjects, the P3 to auditory stimulation was smaller in amplitude than in equally trained musicians without AP (Klein et al., 1984) (P3 is proposed to reflect, among other things, the working memory load; Donchin 1981). In contrast, no group difference was observed with visual stimulation. These results suggest that neuronal mechanisms of visual perception do not differ between AP and non-AP subjects whereas these corresponding mechanisms in auditory modality do differ. The AP subjects may encode pitch in terms of learned labels, categories, rather than by active rehearsal of the presented pitch, these long-term categories facilitating the pitch processing and thus decreasing the working memory load.

Moreover, Besson & Faïta (1996) and Besson et al. (1994), by comparing musicians and non-musicians found that the late positive component (peaking at around 600 ms with a parietal maximum) was remarkably larger for musicians when melodic and harmonic 'deviants' were presented in the end of a melody. No such group difference was present when the terminal tone was delayed, denoting an obvious rhythmic deviance. This suggests that while harmonic and melodic processing may be facilitated by training, rhythmic processing may not be modulated by training.

In addition, it has been shown that musicians' brains differ structurally from those of nonmusicians': The corpus callosum connecting the two hemispheres is thicker in musicians (Schlaug et al., 1995a) and the motor-cortex area innervated by fingers in experienced violinists is enlarged when compared with those of untrained subjects (Elbert et al., 1995). Furthermore, the lateralization of planum temporale (Geschwind & Levitsky, 1968) to the left hemisphere is more pronounced in AP musicians than in other musicians, emphasizing the linguistic component of the AP ability (Schlaug et al., 1995b).

Since none of the above-reviewed studies was aimed at determining the role of pre-attentive memory processes in musical expertise and talent, these questions were addressed in two of the present studies. The first of them, Study VIII, compared the sensory memory functions between AP musicians and non-AP musicians. The subjects' musical background was matched in other respects. The stimuli were, in different blocks, sinusoidal or synthetized piano tones. The frequency difference between the standard and deviant tones was either one semitone or one 'quarter-tone' (half of the semitone), the sounds either belonging to the Western musical scale (C, C sharp) or falling between the note categories (C-, C+, Csharp+). Despite these stimulus parameters, known to be the optimal for AP persons to facilitate their categorical pitch perception of natural instrumental sounds, the MMN amplitudes or latencies did not differ between the groups (Figure 10). The result suggests that the long-term representations of pitch categories were not activated during a parallel reading task in the MMN recordings.

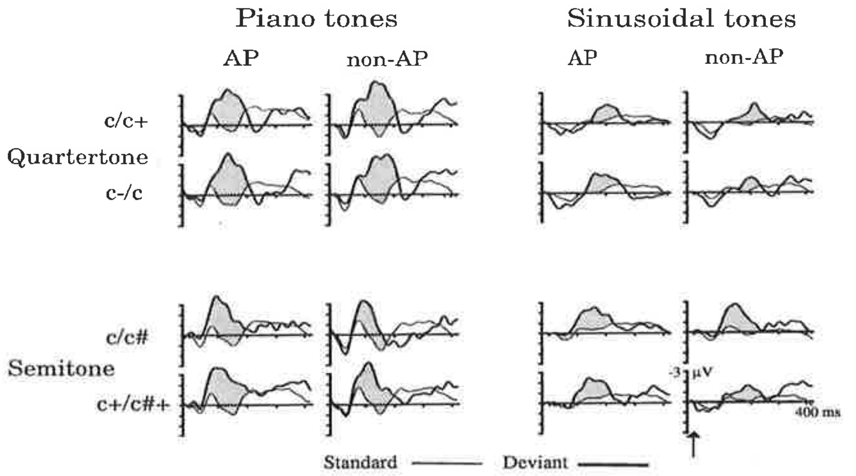


Figure 10. ERPs of the AP and non-AP groups to binaurally presented piano and sinusoidal tones in conditions with different frequency changes as indicated on the left. The thin line represents ERPs to standard stimuli, the thick line ERPs to deviant stimuli. The arrow indicates the stimulus onset and shadowing the presence of MMN.

The tones were of 150 ms duration and the SOA was 690 ms. Altogether four frequency differences were employed between standard and deviant stimuli: 262–269 Hz, 254–262 Hz, 262–277 Hz, and 269–285 Hz. These differences were equal to quarter tone and semitone intervals along the Western musical scale (262 Hz = C^4). The combinations included all possibilities with regard to the tone positions belonging or not belonging to the scale (standard on/off the scale, deviant on/off the scale).

The subjects' performance in the pitch-naming task was tested after the EEG recordings. The subjects were asked to name the pitch and octave of 50 tape-recorded synthetized piano tones (range: C^2 - E^6). The AP subjects correctly named on the average 82% and the non-AP subjects 9% of these test sounds. (Data from Study VIII.)

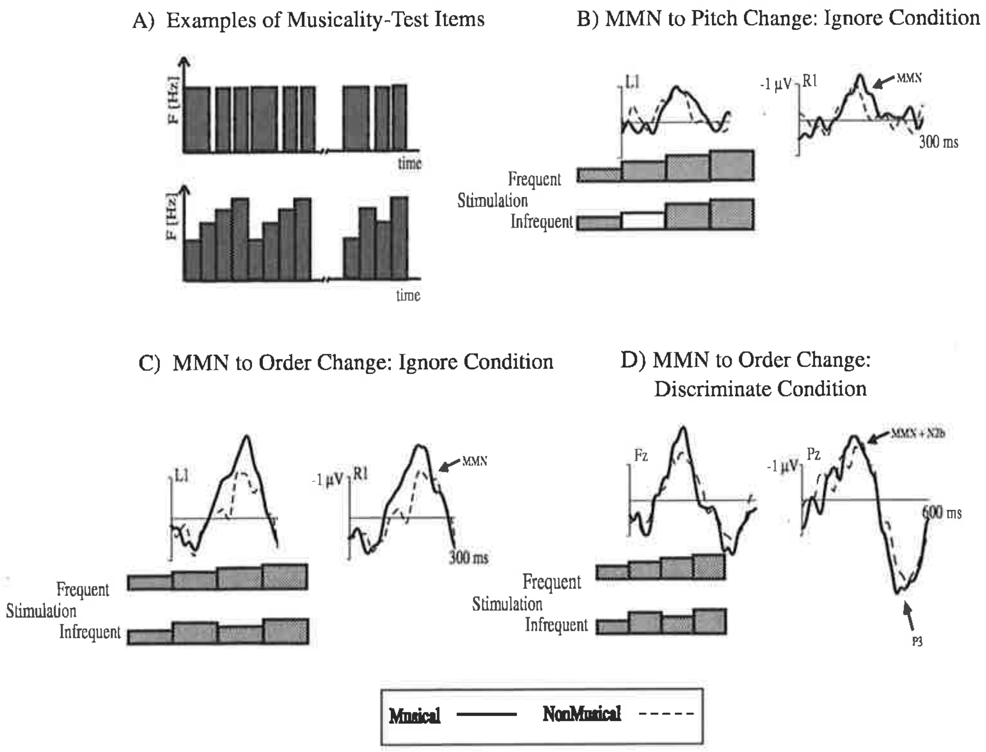
However, recent ERP and MEG data on pre-attentive phoneme processing (phoneme recognition being based on categorizations like AP), complements this result. According to these data, the subjects' native-language environment (Finnish vs. Estonian) affects pre-attentive functions by strengthening the discrimination of phonemes belonging to the native language over phonemes of a foreign language (Näätänen et al., 1997). Corresponding evidence in active paradigm was obtained by Dehaene-Lambertz (1997). Moreover, processing of the most propotypical phoneme within a given phoneme category seems to be pre-attentively facilitated over less prototypical phonemes (Aaltonen et al., in press). Therefore, it might be possible by optimizing stimulus parameters further to activate pre-attentively the memory traces for pitch categories of AP subjects. For instance, stimulus duration may be critical factor for pitch perception of complex sounds (cf. Winkler et al., in press). Alternatively these results might be interpreted as evidencing the preference of the human brain for processing linguistic (phonetic) information in categorical manner. Since in music perception, the relations between successive tones rather than isolated tones are essential, even pre-attentive mechanisms may be more sensitized as a function of musical abilities to encode sound relations.

Therefore, Study IX was conducted to further reveal the differences in pre-attentive auditory processing between subject groups with different musical abilities in perceiving the temporal relations between sounds. This was conducted by comparing neuronal mechanisms of subjects with divergent performances in a cognitively-oriented musicality test (Karma, 1994). This test measures the subjects' ability to structure continuous auditory information into meaningful units (for test examples, see Figure 11A). From the total sample tested, subjects with the best and subjects with the worst test scores were selected for subsequent ERP recordings.

The experiment employed two kinds of stimulation. As discussed in Section 2.1, order reversals in stimulus pairs also elicit the MMN, suggesting that temporal sound properties are also encoded pre-attentively. Since the present test operationalized musicality as an ability to structure temporal information, the main condition of the experiment used order reversals as deviant events. In addition, to reveal the possible differences in the accuracy of the pre-attentive structuring process between the musical and nonmusical subject groups, the tones were not presented as distinct pairs but as a regular continuously repeating tone sequence (such regularity also being encoded by sensory memory; Schröger et al., 1994). In the control condition, the deviant events included a new frequency not present in the standard stimulation. This allowed us to compare the frequency-MMN amplitudes between the groups. This was an especially interesting control taking into account the result of Lang et al. (1990): when subjects were classified on the basis of their pitch-discrimination accuracy, a clear group difference in MMN elicitation was found.

The results indicate that musical subjects had an enhanced MMN amplitude for order-reversed deviants during reading as well as in the discrimination tasks (Figures 11 C and 11D). This suggests that their auditory system encoded the order reversal more accurately. However, this was not the case with frequency deviants (Figure 11 B) with which the MMN amplitude did not differ between the groups.

The present dissociation between the frequency MMN (see Lang et al., 1990) and the order-reversal MMN supports the distinction between sensory and cognitive components of musicality. Moreover, the present result suggests that the cognitive component of musicality may be determined by pre-attentive mechanisms. The present group difference can not be explained by a training effect (see, e.g., Besson & Faïta, 1996; Besson et al., 1994; Elbert et al., 1995; Schlaug et al., 1995a, b) since these subject groups did not differ remarkably in the amount of training in music from each other. It could therefore be concluded that the result indicates the existence of pre-attentive (cortical) basis for the ability to structure auditory information and to find temporal changes in it, this being one essential component in music and speech perception.



A) Examples of Musicality-Test Items

B) MMN to Pitch Change: Ignore Condition

C) MMN to Order Change: Ignore Condition

D) MMN to Order Change: Discriminate Condition

Figure 11A. Example items of the musicality test employed in selecting subjects to Musical and Nonmusical groups. Each of the 40 test items began with a longer sequence in which a short pattern is repeated three or four times (for the sake of brevity, the present examples include only two repetitions). After a short break, a comparison pattern is presented. The subject's task is to judge whether the comparison pattern equals the repeated pattern of the preceding sequence. The patterns are formed either by varying the duration (top row), intensity, or frequency (bottom row) of the tones. In the illustrated examples, the comparison pattern equals the repeated pattern on the top row.

Out of 117 subjects tested, the 15 best and 15 with the poorest scores were selected for ERP recordings. From each group, one subject was rejected because of noisy EEG. The remaining 14 subjects of the Musical group performed in the musicality test at the level of professional musicians (range 38-40/40, average score 39.3). The average score of the 14 subjects in the Nonmusical group was 27.6 points (range 21-30/40).

B. The MMN of Musical and Nonmusical subjects in the Ignore Frequency-Change condition. Here, standard tone sequences which formed C major chords (...C-E-G-C...; 262-330-392-523 Hz) were randomly replaced with deviant events forming a C minor chord (...C-Eflat-G-C...; 262-311-392-523 Hz) (binaural stimulation). The curves are difference waves in which ERPs to frequent tone patterns were subtracted from those to infrequent patterns.

C. The MMN of Musical (continuous line) and Nonmusical (dashed line) subjects to order-reversals of two successive sounds in recursive tone pattern. In standard events, the order of the sounds was ...E-F-G-A..; 330-349-392-440 Hz and in deviant events ...E-G-F-A..; 330-392-349-440 Hz.

D. The MMN+N2b and P3 waves of Musical and Nonmusical subjects in the Discriminate Order-Change condition. (Data from Study IX.)

5.3 Pitch-discrimination accuracy with sinusoidal vs. spectrally rich tones

The ERP evidence summarized above in Sections 3.2 and 5.2 suggests that spectrally complex sounds are at least as accurately encoded in the pre-attentive sensory memory as pure sinusoidal sounds. Study IV (Section 3.2) showed that frequency MMN was elicited by deviant complex tones where only one out of ten harmonic partials was mistuned from its most natural frequency (Figure 6). Furthermore, in Study VIII (Section 5.2), the frequency-MMN amplitude was enchanced with synthesized piano tones (containing multiple harmonics) when compared with MMN evoked by sinusoidal tones with equal frequency change (Figure 10). However, on the basis of those data, no conclusions can be drawn as to whether pitch discrimination under attentive control is more accurate with complex sounds. Furthermore, in Study VIII, in addition to MMN enhancement with piano tones, also N1 enhancement was observed, suggesting that the stimulus loudness might have differed between sinusoidal and piano tones.

To clarify this issue, a very recent study was conducted where both the relationship between MMN elicitation and behavioral discrimination were systematically investigated as a function of sound spectrum (sinusoidal *vs.* harmonically rich sound with three harmonic partials) and the magnitude of the frequency change (2.5, 5, and 10%; standard tone being of 500 Hz and 75 ms) (Tervaniemi et al., in preparation a). These preliminary results indicate that MMN was obtained with all the frequency changes with sinusoidal and harmonically rich sounds, its amplitude being larger and latency earlier with harmonically rich sounds than with sinusoidal tones. In addition, its amplitude reflected the magnitude of frequency deviance (cf. Sams et al., 1985; Lang et al., 1990; Tiitinen et al., 1993). In parallel, the behavioural data indicated that the attentive discrimination of a pitch change is also more accurate with harmonically rich sounds. Thus, the pitch content of spectrally complex stimuli is processed very accurately; this pre-attentive neural encoding even determining the attentive discrimination performance.

The enhanced MMN with harmonically rich sounds may result from parallel encoding of each harmonic partial of the standard, each of them forming mismatches between standard and deviant pitches and thus causing stronger (and sometimes even earlier) MMN responses, as suggested in Study VIII. Alternatively, this result can be explained by "double-coding" of the complex-sound pitch, based on combination of spatial and temporal neural information (Moore, 1989). Previously, MMN additivity has been reported when deviants included changes in more than one sound parameter (e.g., MMN to frequency *and* duration deviance was larger than for pitch *or* duration deviances alone, Levänen et al., 1993; see also Schröger, 1995). The present result showing MMN additivity when two vs. one pitch-encoding mechanisms are involved might reflect that memory traces incorporate spatial and temporal pitch information when available, the neural codes being additive even within one sound parameter (e.g., pitch). This interpretation is supported by ERP and behavioral results received during attentive listening, indicating that separate sound parameters are first processed in parallel and theafter combined as a sound object (Thompson, 1994; Woods et al., 1994; cf. the feature-integration theory in visual modality by Treisman & Gelade, 1980.) According to recent MEG evidence, these successive phases may even have separate neuronal generators (Levänen et al., 1996).

6 ACTIVATED BRAIN STRUCTURES BY CHANGES IN COMPLEX SOUNDS

As reviewed in Section 1.3, the MMN to changes in sinusoidal tones is generated mainly in the auditory cortex or in its immediate vicinity. Within the auditory cortex, the location of the MMN generator seems to differ depending on the deviating parameter (e.g., intensity, duration, frequency; Giard et al., 1995). Moreover, the frequency-MMN generators are tonotopically organized (Tiitinen et al., 1993). These results suggest that the memory traces for different separate sound features and even for their different values could have separate neural loci. The evidence to be discussed in the following will shed light concerning the locations of MMN generators when more complex stimulus material is employed.

6.1 Functional specialization of the auditory cortex

The neural organization of the visual cortex is known to be differentiated to process stimuli with specific visual features and various degrees of complexity (Hubel, 1988; Zeki, 1993). Consequently, it was of interest to determine whether location of MMN generators depends on stimulus complexity. This would suggest a similar kind of specialization at different areas in the auditory cortex.

In STUDY X, MEG recordings were conducted with three kinds of stimuli, each of them having identical frequency change embedded in them: single sinusoidal tones, parallel chords, and sequential chords (FIGURE 12A). A change in all of them elicited the MMNm response. The MMN strength or latency did not differ between the three different stimuli. However, while comparing the MMNm generator locations as indicated by ECDs as a function of the stimulus complexity, it was found that the MMNm generator was, on the average, 10 mm deeper (more medial) in the auditory cortex for the sequential and parallel chords than for the single tones (FIGURE 12B). This suggests that within the auditory cortex, there are neuronal populations specialized in encoding spectrally or temporally complex information. Furthermore, recent MEG data suggest that frequency changes of equal magnitude embedded in phonemes and chords might be pre-attentively encoded by separate neuronal populations within both cortices (Kujala, 1997). The generator loci of MMNm to phoneme changes was located in both hemispheres superior to that of the MMN to chord changes. The generator locus of P1m (one of the earliest cortical responses) did not differ between these two stimulus types.

Specialization of auditory cortex as a function of stimulus complexity can be also inferred from several frequency-MMN studies conducted with EEG. In those experiments, by employing more complex stimuli, a centrally maximal MMN without polarity reversal at mastoid leads was obtained (Saarinen et al., 1992; Study II). This was observed instead of a frontally maximal MMN with polarity reversal as seen with single sinusoidal tones (Paavilainen et al., 1993; Schröger, 1994). This suggests differently located or oriented generators for complex sounds than for simple tones. In addition, the preliminary MEG results of Tervaniemi et al. (in preparation b) indicate that this kind of specialization of the auditory cortex is not limited to frequency coding only but that it may be observed for intensity coding as well.

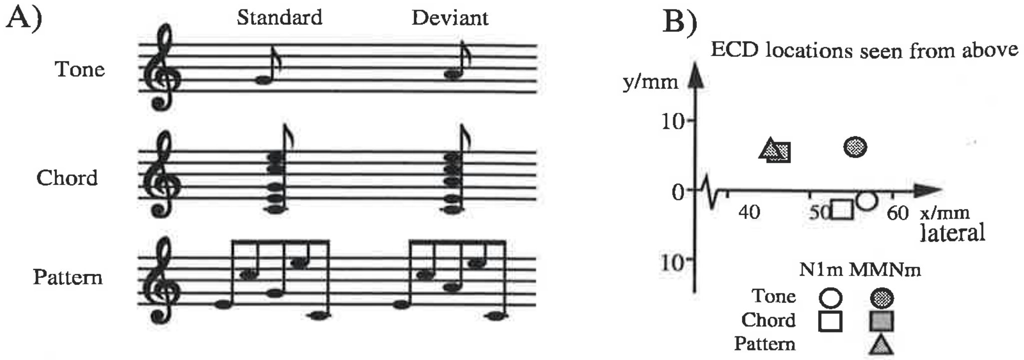


Figure 12A. Stimuli of Study XII. An identical frequency change (392 Hz (G^4) in standards *vs.* 440 Hz (A^4) in deviants) was presented in three contexts in order to compare MMNm generator locations between them. In the tone condition, both stimuli were single sinusoids. In the chord condition, the standard stimulus consisted of five simultaneously presented sinusoids (C major *vs.* A minor). In the pattern condition, the patterns consisted of the five serially presented frequencies belonging to the C major *vs.* A minor chords. The tones were delivered to reading subjects' left ear via a plastic tube and an earpiece.

B. Locations of ECDs for the N1m to the standard tone and for the chord and mismatch responses to the deviant tone, chord, and sound pattern in the auditory cortex of the right hemisphere (average across 10 subjects). The *x* axis is defined by the line connecting the left and right preauricular points and the *y* axis is oriented towards the nasion. (Data from Study X.)

However, the recent results of Csépe et al. (1997) comparing MMNm generator locations between stimulus pairs *vs.* single sounds (with identical frequency change in both) seem to contradict the results of Study X. These authors found that the MMMm generator for paired-sound changes was, on the average, 5 mm more *lateral* to MMNm for single sounds. In contrast, the data from Study XII indicated that with more complex stimulation, MMNm is generated, on the average, 10 mm more *medial* to MMNm for single tones. Moreover, in the data of Hari et al. (1992), the generator loci of MMNm for paired and single tones did not differ. Perhaps tone pairs are not complex enough that changes in them would necessarily activate the same complex-sound processing mechanisms as changes in chords with five parallel or sequential frequency elements. In all, it seems that further experimental work (preferably with a whole-head magnetometer providing the most accurate localization results) is necessary for resolving the issue of the functional specialization of the auditory cortex.

7 EPILOGUE

The data of the present thesis, gathered by recording event-related electric and magnetic brain activity noninvasively from human subjects, imply, first of all, that remarkably complex stimulus entities are encoded pre-attentively. They indicate also that expectations concerning the continuation of the auditory information may be pre-attentively formed. It seems that in natural acoustic environments, the auditory system performs relatively complex analysis before directing conscious attention towards the changes. During that analysis, regularity in sounds is encoded so that despite continuous change in surrounding sounds the listener's attention is not caught by new sounds if they fit into the general context and do not violate the regularity. However, any deviation from these intrinsically formed 'rules' elicits the change-detection response. Therefore, the present findings support the views in cognitive psychology emphasizing the importance pre-attentive processes in perception (e.g., Massaro, 1975; Näätänen, 1992).

Second, the results indirectly suggest that auditory stimulation which contains natural overtone series may be even more accurately encoded than stimulation with less spectral information. More recent results confirmed this finding which is probably due to parallel encoding of all stimulus information by separate neural mechanisms. Thus the auditory system benefits from increased information since its broad capacity can utilize all the information available in change detection and reorientation. However, it should be noted that in all the present studies, the subjects' primary task was to read a book. It might be argued that during ERP recordings, they were not fully concentrated on reading but had some attentional capacity directed toward the sound stimulation which, in turn, enhanced the responses (cf., Alain et al., in press). On the other hand, if involuntary attention enhanced the MMN only with complex stimuli when the experiment included both simple and complex stimuli (Study VIII) this further supports the hypothesis about the preference of auditory system to process stimulation with high informational content.

Third, the present results show that pre-attentive brain functions may be altered by stimulus duration or SOA. This was evidenced by omission MMN that were elicited only with stimuli presented with < 150 ms SOA (single sounds) or < 300 ms SOA (paired sounds). A different pattern of results was found when a frequency change within a continuous spectrally and temporally complex tone was presented. Prolonged stimulus duration facilitated an attention switch towards the change until the time difference between the stimulus onset and the change onset exceeded 180 ms. These results confirm the existence of pre-attentive integration mechanism for auditory information, previously evident only in behavioral studies, and, moreover indicate that its functions differ between discrete and continuous stimulation.

Fourth, the present results suggest that the cortical areas encoding the auditory information may be specialized as a function of stimulus complexity within one hemisphere. Related functional specialization of neuronal networks was recently revealed by MEG recordings between the two hemispheres for phonetic *vs.* musical information processing. According to these results, the MMNm was significantly stronger in the left hemisphere for phoneme changes and in right hemisphere for the sinusoidal-tone changes, both changes being equal in frequency (Lehtokoski et al., in preparation). Although direct hemispheric comparisons are not warranted due to profound difference in the stimulus structure complexity, it is possible that the long-term memory traces for phonemes were activated by the present phonetic stimulation causing the stronger MMNm in the left hemisphere. A parallel MEG study employed phonemes *vs.* chords in separate conditions, identical frequency change being embedded in their deviants (Kujala, 1997). There, chords elicited stronger right-hemisphere MMNm whereas for phonemes there was no hemispheric dominance. This pattern of lateralization was not affected by the ear of stimulation. These results together promote the use of either spectrally or temporally complex stimuli especially if the main interest is to investigate the neurophysiological basis of human abilities like speech or music perception. For instance, the hemispheric lateralization regarding the temporal information processing is highly controversial issue which could be possibly solved by appropriate magnetic MMN recordings or electric MMN recordings with high-resolution EEG (e.g., Rinne et al., in preparation).

Fifth, the data show that with the complex stimulation employed in the present studies, differences in pre-attentive neural functions between subjects were associated with differences between their discrimination accuracy as measured by separate behavioral tasks. This result is promising since, as discussed above, human auditory system may encode complex, natural information even more accurately than e.g., sinusoidal tone information with which such a correspondence between pre-attentive and attentive auditory processing has been shown previously. Although the present data reveal differences on group level only, this kind of stimulation could in future be successfully applied in clinical (e.g., see Kraus et al. 1995; Ponton et al., 1995) and possibly also in educational (Alho & Näätänen, 1995) settings to reveal individual differences in neural mechanisms of auditory perception and learning. This approach would be valuable especially with regard to patients and children with whom active paradigms may not be reliable due to disorders in voluntary attention and/or communication. However, the stimuli employed in the present studies could be further optimized for the work conducted with individual subjects/ patients. For instance, the stimulation should consist of either spectrally or temporally complex but still discrete stimuli to yield maximally clear ERP signals (Schröger, submitted). The sound pressure level should also be adjusted for each subject individually, relative to his/her hearing level to avoid artefactual MMN differences due to differences in stimulation loudness (Salo et al., submitted, however, see Schröger, 1994). Moreover, the quantification procedures for MMN latency and amplitude should be optimized to reveal sensitively but reliably inter-individual differences (Joutsiniemi et al., submitted; Lang et al., 1995). It should be noted that even the studies conducted at the group level by comparing groups with presumed differences in perceptual abilities would benefit from these methodological improvements.

Furthermore, the present thesis illuminated the neural processing of auditory information perceived in illusory way. It appeared that despite insufficient spectral information as provided with missing-fundamental tones, the perceived pitch is pre-attentively encoded to match the missing-fundamental frequency. In contrast, with regard to binaural octave illusion it appeared that the pre-attentive neural mechanisms are not sufficient in encoding the perceived illusion but that they rather rely on physical stimulus features. These results emphasize the role of pre-attentive processing in natural acoustical environment where the physical signal is often incomplete. Even without voluntary attention the signal can be interpreted as if it had all elements in it. However, when the auditory information is delivered more artificially through headphones with both ears receiving different input, the information content is not interpreted in illusory way without further attentional processes.

In sum, the present thesis underlines the importance of pre-attentive processing of spectrally and temporally complex auditory information. Moreover, it promotes the utility of MMN recordings in revealing the neurocognitive functions behind perception of nonverbal auditory information and even in determining the interindividual differences in them.

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Appendix: General methods

Experimental Procedure

Altogether 158 paid subjects (72 males) participated in the experiments of the present thesis. The age range of the subjects was 18–37 years. During the experiments, the subject was sitting on a reclining chair, instructed to concentrate on reading and to ignore the stimulation. In addition, Studies VII and IX included conditions in which subjects were instructed to press a response key when they detected a deviant sound or sound pattern.

The auditory stimulation was delivered to subjects via headphones (EEG experiments, Studies I–IV and VI-IX) or via plug and an ear tube (MEG experiments, Studies V and X). The stimulus intensity was adjusted in each experiment to comfortable hearing level (70–75 dB SPL) so that it did not disturb the subjects. Stimulus parameters (frequency, spectral structure, duration, inter-stimulus interval) specific to each experiment are indicated in the figure legends of those figures illustrating the corresponding data.

Data Recording and Analysis in EEG Experiments, Studies I–IV and VI-IX

The recordings were conducted in electrically shielded and sound-attenuated chamber (Euroshield Ltd). The EEG was recorded with 0.1–100 Hz bandpass with Ag-AgCl electrodes which were attached to 5-10 scalp locations: 3 electrodes were placed to the midline: Fz (over the frontal area), Cz (over the vertex), and Pz (over the parietal area). In addition, in studies III, IV, VI, and IX, 6 electrodes were placed equidistantly along the tilted coronal line connecting the mastoids through Fz. These lateral electrodes were called LM (mastoid), L2, and L1 on the left, and RM (mastoid), R2, and R1 on the right.

In all the studies, the electro-oculogram (EOG) was recorded with two electrodes, one attached to the outer canthus of the right eye to monitor artefacts caused by horizontal eye movements, and the other to Fpz (on the forehead) to record artefacts caused by vertical eye movements. The nose served as a reference for all electrodes.

The recorded EEG was stored on a computer disc for off-line averaging. Digitization rates were from 200 to 500 Hz, depending on the study. The duration of the averaged EEG epochs varied across studies, depending on the stimulus rate, from 450 to 1100 ms. ERPs were averaged separately for the standard and deviant stimuli. After averaging, the data were digitally either low pass (30 Hz) or bandpass (1-30 Hz) filtered. Epochs with EEG or EOG changes exceeding 150 µV were automatically rejected. Prestimulus periods (or the period preceding the presentation of a deviant sound element) of 50–275 ms (depending on the stimulus type) were used as the baseline.

Data recording and analysis in MEG Experiments, Studies V and X

The recordings were conducted in the magnetically shielded and sound-attenuated chamber in the Low Temperature Laboratory, Helsinki University of Technology. A 122-channel whole-head magnetometer (Neuromag Ltd), recording two orthogonal components of the magnetic field gradient with planar gradiometers in 61 locations, was used. The data were collected with the sampling rate of 397 and 398 Hz and passband of 0.01-90 and 0.01-100 Hz in Studies V and X, respectively. After on-line averaging, responses were digitally filtered (bandpass 2-20 and 1-20 Hz in Studies V and X, respectively). For artefact rejection, the EOG was monitored from the left canthus and just above the left eye. All epochs with the variation exceeding 150 μV (EOG channels) or 1500 fT/cm (MEG channels)were automatically omitted.

MMN Analysis

The MMN amplitude and latency were determined from difference curves which are obtained by subtracting ERP to standard stimuli from corresponding ERP to deviant stimuli. In Studies I–IV and VI, VIII, and IX, the MMN amplitude was quantified as a mean amplitude of a 20–100 ms integration window of the difference curve of each individual subject, separately for all the experimental conditions. This integration window was centered at the latency of the most negative value as determined in the grand-average (across subjects) difference wave between 100 and 300 ms after the deviant-stimulus onset. In Study VII, MMN amplitude was quantified as an integrated amplitude between 100 and 300 ms after deviant stimulus element presentation. In addition, in Studies I, VII, VIII, and X, the MMN peak latency was determined as the latency of the most negative value of the difference curve. Thereafter, the significance of the MMN was tested by t-tests comparing the MMN amplitude to zero level. Furthermore, the existence of differences in MMN latency, amplitude, and scalp topography between experimental conditions and/or subject groups were statistically tested by analysis of variance (ANOVAs).

In Studies V and X, the MMNm generator locus was modelled by one equivalent current dipole (ECDs; dipoles that optimally, in the least-squares sense, reproduce experimentally obtained magnetic field patterns in each hemisphere). Before the measurements, the magnetometer position with respect to the head was determined by recording the magnetic fields produced by currents fed into indicator coils at known head locations. In Study X, ECDs were determined in a spherical head model by using magnetic responses in 44 channels centered at the approximate location of contralateral right auditory cortex and 26-44 channels centered over the ipsilateral left auditory cortex. In Study V, all channels were in use. The resulting ECD explained at least 64 % and with the majority of the subjects, 80 % of the recorded signal. In Study X, MMNm generator loci were compared across experimental conditions by ANOVA.