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Functional Specialization of the Human Auditory Cortex in Processing Phonetic and Musical Sounds: A Magnetoencephalographic (MEG) Study

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Functional specialization of the human auditory cortex in processing phonetic vs musical sounds was investigated. While subjects watched a silent self-selected movie, they were presented with sequences consisting of frequent and infrequent phonemes (/e/ and /o/, respectively) or chords (A major and A minor, respectively). The subjects' brain responses to these sounds were recorded with a 122-channel whole-head magnetometer. The data indicated that within the right hemisphere, the magnetoencephalographic (MEG) counterpart MMNm of the mismatch negativity (MMN) elicited by an infrequent chord change was stronger than the MMNm elicited by a phoneme change. Within the left hemisphere, the MMNm strength for a chord vs phoneme change did not significantly differ. Furthermore, the MMNm sources for the phoneme and chord changes were posterior to the P1m sources generated at or near the primary auditory areas. In addition, the MMNm source for a phoneme change was superior to that for the chord change in both hemispheres. The data thus provide evidence for spatially distinct cortical areas in both hemispheres specialized in representing phonetic and musical sounds. © 1999 Academic Press

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INTRODUCTION

The neuronal architecture behind auditory perception is functionally specialized in many different ways. Interhemispheric specialization refers to how auditory cortices in the left and right hemispheres differentially process verbal and nonverbal auditory information. Intrahemispheric specialization refers to the functional specialization of some cortical area within a hemisphere to process certain kinds of auditory information.

The first evidence for interhemispheric specialization of auditory information processing was obtained more than a hundred years ago when it was shown that left-hemisphere lesions lead to disturbances in speech perception (Wernicke, 1874). More recently, right-hemisphere lesions were shown to deteriorate music processing (for a review, see Benton, 1977). Later studies recording electrical brain activity and regional cerebral blood flow and metabolism from healthy subjects confirmed that phonetic information is processed primarily in the left hemisphere and that nonphonetic auditory information is processed primarily in the right hemisphere (Auzou *et al.*, 1995; Binder *et al.*, 1995; Mazoyer *et al.*, 1993; Mazziotta *et al.*, 1982; Näätänen *et al.*, 1997; Petersen *et al.*, 1988; Zatorre *et al.*, 1992). However, there are also contradicting results, especially regarding the predominant role of the right hemisphere in music processing in musically trained subjects (Bever and Chiarello, 1974; Gordon, 1970; Hirskowitz *et al.*, 1978; Nicholls, 1996; Paquette *et al.*, 1996; Sidtis, 1984).

The intrahemispheric specialization of different areas of the auditory cortex could be revealed with human subjects only after the establishment of the modern methods in brain research less than 20 years ago. Most consistently, the tonotopic organization of the cochlea, maintained up to the auditory cortex in nonhuman species (for reviews, see Buser and Imbert, 1992; Pickles, 1988), was demonstrated in humans with magnetoencephalography (MEG) (Pantev *et al.*, 1995; Romani *et al.*, 1982; Tiitinen *et al.*, 1993; Yamamoto *et al.*, 1992), positron emission tomography (PET) (Lauter *et al.*, 1985), and functional magnetic resonance imaging (fMRI) (Wessinger *et al.*, 1997). In addition, MEG recordings indicated that activation caused by phonetic formant structure depends on the tonotopic organization revealed by pure-tone stimulation (Diesch and Luce, 1997). A very recent MEG study suggests that there are topographically organized maps in the human auditory cortices also for the temporal (periodicity) aspect of frequency information (Langner *et al.*, 1998; see also Pantev *et al.*, 1989).

Furthermore, MEG recordings indicated that the source location of N1m responses (which peak at about

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100 ms from stimulus onset) for phoneme /a/ differs from those of consonant-vowel (CV) syllables /na/, /ka/, and /ha/ in the left but not in the right hemisphere, indicating both inter- and intrahemispheric specialization (Kuriki and Murase, 1989; Kuriki *et al.,* 1995). A more recent study indicated that frequency changes within repetitive musical stimuli (parallel and serial chords) are processed in the right hemisphere by a neuronal population spatially distinct from that processing frequency changes in a pure sinusoidal tone (Alho *et al.,* 1996). This result was obtained by recording the magnetic counterpart of the mismatch negativity (MMNm) event-related potential (ERP), indexing preattentive change detection when a cortical memory trace representing the features of a repeating stimulus ("standard") and the features of the incoming ("deviant") stimulus differ (Näätänen, 1992).

The present study was conducted to determine whether inter- and intrahemispheric mechanisms for phonetic and nonphonetic auditory information processing differ as early as at the preattentive level. MEG with excellent temporal and spatial resolution was utilized to reveal the loci and strengths of MMNm generators for spectral changes in phonetic and nonphonetic information.

MATERIALS AND METHODS

Subjects

Fourteen healthy Finnish-speaking adults volunteered as subjects; data from two of them were discarded from further analysis because of the low signal-to-noise ratio. The remaining 12 subjects (6 males, age 20–31 years; mean 24 years) were all right-handed and musically untrained.

Stimuli and Procedure

Phonemes and chords were presented in separate sequences. In the phoneme sequences, a frequently presented ($P = 0.8$), "standard" stimulus was the Finnish phoneme /e/ (approximately as in "set") and a infrequently occurring "deviant" stimulus ($P = 0.2$) was /o/ (approximately as in "door"). In the chord sequences, the standard stimulus was the A major chord and the deviant stimulus the A minor chord. In both sequences, the deviant stimuli differed from the standard stimuli in their second spectral component. The chords were built so that the physical change from A major to A minor would approximate the change from /e/ to /o/, that is, equal to one octave. The frequencies of the different phoneme formants and chord tones are given in Table 1. The stimulus duration was 200 ms including 10-ms rise and fall times. The stimulus intensity was 50 dB above to the subjective hearing level. The constant offset-to-onset interstimulus interval was 300 ms.

TABLE 1

The Frequencies Employed in Constructing the Phoneme (Upper Panel) and Chord (Lower Panel) Stimulation

Phonemes	Formant 1	Formant 2	Formant 3	Formant 4
Standard /e/	450 Hz	1866 Hz	2540 Hz	3500 Hz
Deviant /o/	450 Hz	921 Hz	2540 Hz	3500 Hz
Chords	Tone 1	Tone 2	Tone 3	Tone 4
Standard A major	440 Hz	1109 Hz	1319 Hz	1760 Hz
Deviant A minor	440 Hz	523 Hz	1319 Hz	1760 Hz

The semisynthetic phonemes were generated based on the vocal-tract model (Alku, 1992) by synthesizing the natural glottal excitation (see Näätänen *et al.,* 1997). The chords were composed of four sinusoidal tones with a PC-based NeuroStim-program (NeuroScan Inc.). Stimuli were delivered with the NeuroStim program through plastic tubes and earpieces, frequency distortions being compensated for with a correction filter. Phonemes and chords were delivered in three conditions either binaurally or monaurally to the left or to the right ear, the experiment thus including altogether six conditions. The order of conditions was counterbalanced between the subjects. They were instructed to ignore the stimuli while watching a silent self-selected movie on a monitor at the distance of about 2 m.

MEG Recordings

The MEG was recorded in a magnetically shielded room (Euroshield Ltd.) in the BioMag Laboratory of the Helsinki University Central Hospital with a helmet-shaped 122-channel whole-head magnetometer (Neuromag Ltd.). The sensor array consists of 61 dual-sensor units, each with two orthogonal planar gradiometers recording the maximal signal directly above a source. Before the experiment, the positions of three marker coils placed on the scalp were determined in relation to three anatomical landmark points (the nasion and both preauricular points) with an Isotrak 3D-digitizer (Polhemus Inc.). The position of the magnetometer with respect to the head was determined for each condition by feeding currents to the marker coils and locating them prior to the beginning of each pair of experimental conditions: before the binaural phoneme and chord conditions and again before both monaural phoneme and chord conditions.

The MEG epochs (passband 0.1–100 Hz and sampling rate 398 Hz), starting 100 ms before (prestimulus baseline) and ending 500 ms after each stimulus onset, were on-line averaged separately for standard and deviant stimuli. Horizontal and vertical eye movements were monitored with electrooculography (EOG) electrodes placed above and below the left eye and lateral to the eyes. MEG epochs with deflections larger

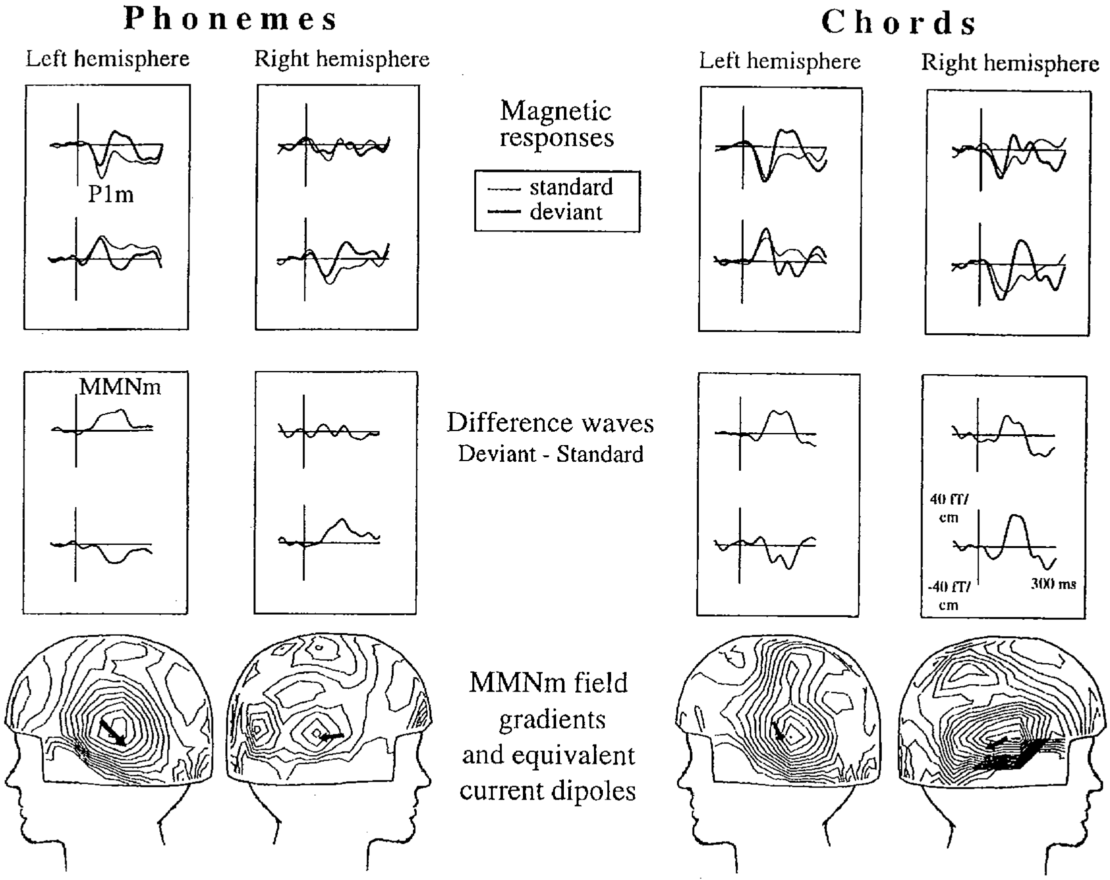


FIG. 1. MMNm responses in an individual subject elicited by binaural standard (thin line) and deviant (thick line) phonemes (left panel) and chords (right panel) and corresponding deviant-standard difference waves recorded above the left and right auditory cortices. MMNm field gradients (difference between the adjacent lines 2 fT/cm) and ECDs (arrows) are illustrated on bottom.

than 150 μV or 1500 fT/cm in any of the EOG or MEG channels, respectively, were rejected from the averaging because they were contaminated with extracerebral artefacts such as eye movement, blinks, or muscle activity. In each condition, at least 120 deviant responses were collected.

Data Analysis

The responses for both hemispheres were filtered digitally with a passband of 0–20 Hz (6 subjects), 1–20 Hz (2 subjects), and 2–20 Hz (4 subjects). The passband was selected so that the response returned to the 0 fT/cm baseline during the epoch which was 500-ms in duration.

For each subject and condition, equivalent current dipoles (ECDs) were determined for the P1m, which was the most prominent response to standard stimuli (due to fast stimulation rate, N1m was of very small amplitude). The ECDs for the MMNm were determined from the deviant-stimulus response minus standard-stimulus response subtraction waves. In ECD modeling, a spherical head model was used (Hämäläinen *et al.*, 1993). The center of the model sphere was placed 45 mm above the origin of the coordinate system defined so that the x-axis pointed from the left to the right preauricular point, the y-axis was perpendicular to the x-axis and passed through the nasion; the z-axis pointed upwards (see Fig. 3). In auditory MEG studies, this placement of the sphere is the most commonly used since such sphere approximately matches the shape of the head above the region under interest. Although this model introduces systematic error in the estimated dipole location, its use does not prevent us from discriminating different sources from each other.

In each condition, one ECD for P1m between 40 and 100 ms and one ECD for MMNm between 100 and 250 ms was fitted separately for the left and right hemispheres using a fixed subset of 30 MEG-channels over each auditory cortex. Each ECD was determined so that it explained optimally the recorded magnetic field and had largest dipole moment during the predefined time range. All ECDs accepted for statistical analysis explained over 60% of the measured magnetic field and were oriented correctly with respect to the corresponding electric component (P1m ECD producing positivity and MMNm ECD producing negativity at the frontal and central scalp areas). In the monaural conditions,

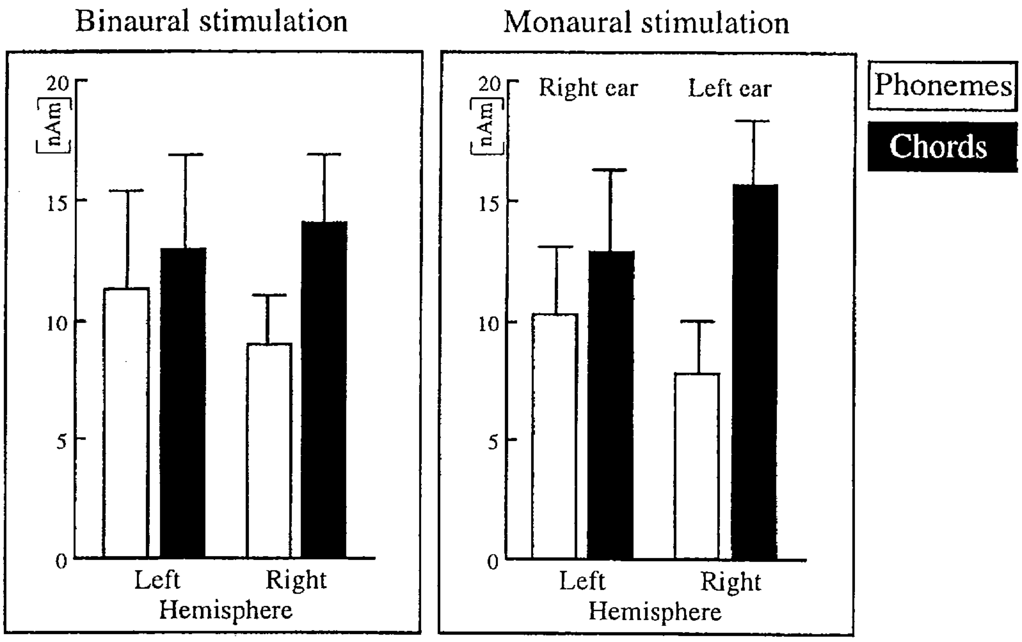


FIG. 2. The mean ECD strengths (12 subjects) of MMNm elicited by phonetic and chord changes in different experimental conditions. The error bars on the top of each bar indicate the half range of the standard errors of the mean.

some ECDs explained poorly the magnetic fields over the hemisphere ipsilateral to the stimulated ear. Therefore, no ipsilateral ECDs for monaural stimulation were analyzed and only contralateral ECDs from the monaural condition where included to the analyses of variance. The mean goodness of fit in each condition is presented in Table 2. For both P1m and MMNm, 81% of the confidence volumes were below 4 cm^3 (of which 68% for P1m and 50% for MMNm were below 1 cm^3).

The strengths and locations of the ECDs and their latencies were compared in ANOVAs for repeated measures with factors stimulus type (phoneme/chord), stimulus location (monaural/binaural), and hemisphere (right/left). Following this 3-way ANOVA, subsequent analyses to be specified under Results were conducted. In addition, a 4-way ANOVA was conducted to compare the P1m and MMNm ECD locations with factors component (P1m/MMNm), stimulus type (phoneme/chord), stimulus location (monaural/binaural), and hemisphere (right/left).

RESULTS AND DISCUSSION

Responses recorded over the left and right auditory cortices of a typical subject are shown in Fig. 1. These responses demonstrate that both the standard and the deviant stimuli elicited the P1m response. The P1m peaked, on the average, between 74 and 83 ms with phoneme stimulation and between 68 and 83 ms with chord stimulation (determined as time point of the maximal dipole strength). The P1m latency was shorter with monaural than binaural stimulation irrespective of the stimulus type or hemisphere [$F(1, 11) = 7.7$, $P < 0.05$; 3-way ANOVA with factors stimulus type, hemisphere, and location].

With deviant stimuli, the P1m was followed by the MMNm. The MMNm peaked, on the average, between 139 and 146 ms with phoneme stimulation and between 140 and 162 ms with chord stimulation (determined as time point of the maximal dipole strength). The MMNm latency was not affected by the type of stimulation (phoneme vs chord), hemisphere (left vs right), or stimulus location (monaural/binaural).

MMNm Strength

As Fig. 2 shows, there was a tendency of the MMNm dipole moment to be stronger with chord stimulation in the right than in the left hemisphere and with phoneme stimulation in the left than in the right hemisphere [stimulus type × hemisphere interaction: $F(1, 11) = 3.7$, $P < 0.08$; 3-way ANOVA with factors stimulus type, stimulus location, and hemisphere; see also Table 2]. A further analysis indicated that this tendency resulted from a significantly stronger MMNm dipole moment for chord change than for phoneme change within the right hemisphere [main effect of stimulus type, $F(1, 11) = 28.7$, $P < 0.001$; 2-way ANOVA with factors stimulus type and location]. In the corresponding ANOVA within the left hemisphere, there was no significant difference between MMNm strength between the stimulus types. In general, the stimulus type had a significant effect on the MMNm dipole moment, which was, irrespective of the stimulated ear, stronger for the chords than for the

TABLE 2

The ECD Strengths, Goodnesses of Fits, and Coordinates of P1m and MMNm with Binaural (Upper Panel) and Monaural Stimulation (Bottom Panel; Only Ipsilateral Values Are Represented)

	Binaural stimulation									
	Left hemisphere					Right hemisphere				
	Dipole moment [nAm]	Goodness of fit [%]	*x* [mm]	*y* [mm]	*z* [mm]	Dipole moment [nAm]	Goodness of fit [%]	*x* [mm]	*y* [mm]	*z* [mm]
P1m										
Phoneme	14.6	93.7	−44.4	9.4	57.6	12.5	92.2	50.8	15.9	54.6
Chord	12.2	93.4	−45.5	10.3	56.8	11.5	93.0	52.0	15.6	53.6
MMNm										
Phoneme	11.3	85.5	−43.9	7.0	59.1	9.0	76.5	48.4	8.6	57.8
Chord	12.9	81.6	−42.1	8.4	56.6	14.0	85.0	49.0	13.4	51.6
	Monaural stimulation									
P1m										
Phoneme	12.2	92.4	−44.6	10.2	54.3	10.2	90.5	49.6	16.0	53.3
Chord	9.7	89.7	−45.1	10.9	59.2	8.2	90.5	51.6	16.5	53.2
MMNm										
Phoneme	10.3	72.4	−41.2	7.1	57.2	7.8	78.4	51.8	11.6	55.4
Chord	12.8	84.0	−45.3	9.9	57.6	15.6	88.6	49.9	12.5	51.6

phonemes [main effect of Stimulus Type, $F(1, 11) = 22.6$, $P < 0.001$; 2-way ANOVA with factors stimulus type and location].

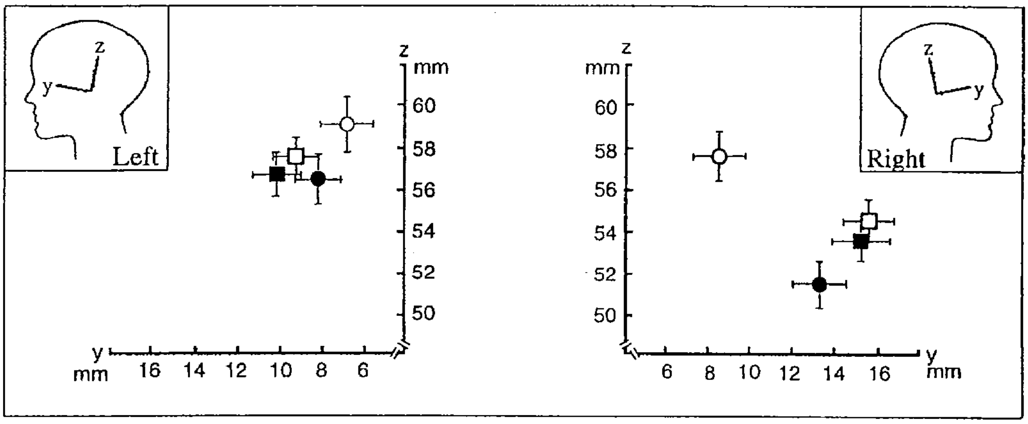
According to the present data, chord changes are processed more vigorously than phoneme changes within the right hemisphere, whereas within the left hemisphere there is no such difference. This suggests that even at the preattentive level, the right hemisphere is specialized in processing musical rather than nonmusical sound material. In contrast, the left hemisphere seems not to have such preattentively activated predominance for phonetic material. Very recently, however, significantly stronger MMNm and MMN were found in the left hemisphere for phoneme changes and in the right hemisphere for sinusoidal-tone changes (Lehtokoski *et al.*, unpublished data; Näätänen *et al.*, 1997; Rinne *et al.*, 1997). The difference between those results and the present data could be caused by differences in stimulation. The present study used stimuli of 200-ms duration, whereas the studies displaying predominantly left-hemispheric MMN(m) to phoneme changes used stimuli of 400-ms duration. Although natural speech consists of phonemes shorter than 100 ms, isolated semisynthetic stimuli presented in repetitive manner might be processed fully as phonemes only if sound duration exceeds 200 ms.

P1m and MMNm Generator Loci

Figure 3 presents the mean ECD loci for the P1m and MMNm for chords and phonemes. The MMNm source locations were significantly posterior to the P1m source locations in both hemispheres and with both stimulus types [main effect of component in a 4-way ANOVA with factors stimulus type, stimulus location (y axis), hemisphere, and component; $F(1, 11) = 11.4$, $P < 0.01$]. Moreover, the phoneme-MMNm source was superior to and chord-MMNm source inferior to the P1m sources. This resulted in a significant interaction between stimulus and component in a 4-way ANOVA with factors stimulus type, stimulus location (z axis), hemisphere, and component [$F(1, 11) = 10.9$, $P < 0.01$]. In contrast, the source locations between chord-P1m and phoneme-P1m did not statistically differ.

The data thus suggest that the generator loci of the P1m and MMNm components differed from each other, the MMNm sources being posterior to the P1m sources for both stimulus types. This pattern of data were not affected by the site of stimulation (left vs right, monaural vs binaural) or by the hemisphere (left vs right). Since P1m sources are located at or near the primary auditory cortex (Liégeois-Chauvel *et al.*, 1994; Mäkelä *et al.*, 1994; Pantev *et al.*, 1995), this suggests that the present spectrally complex stimuli activated cortical areas behind the primary auditory areas. This finding is in line with the previous evidence especially for the left hemisphere where Wernicke's area is located posteriorly to the primary auditory cortex, its lesions resulting in receptive aphasias. Interestingly, it has been shown that while aphasic patients with left-hemisphere lesions displayed an MMN to frequency change in a sinusoidal tone irrespective of the position of their lesioned brain area (anterior/posterior), no MMN to phonetic changes was observed in patients with posterior lesions causing receptive aphasia while the pa-

Binaural stimulation



Right-ear stimuli

Monaural stimulation

Left-ear stimuli

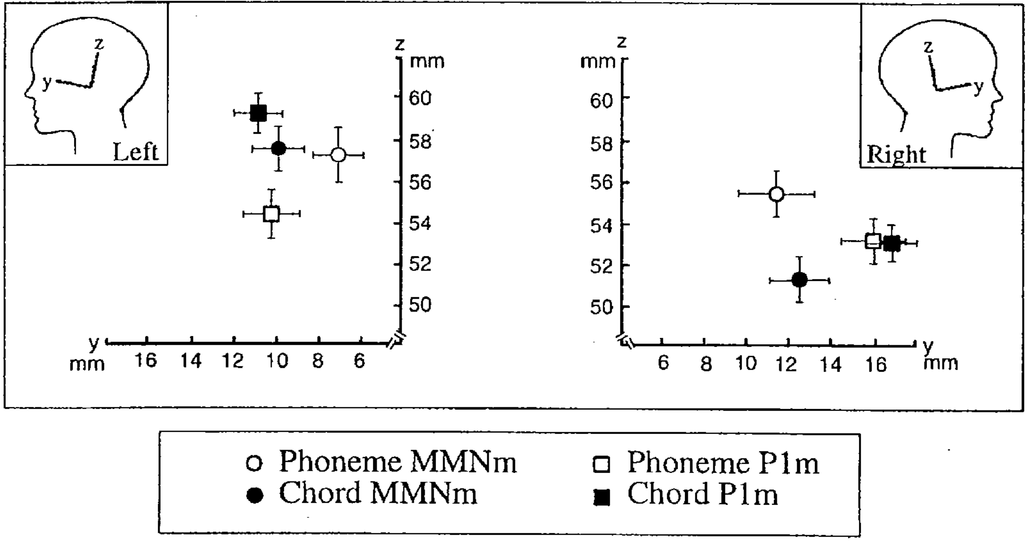


FIG. 3. The mean ECD loci (12 subjects) on a sagittal plane modelled for the P1m to standard phonemes and chords and for the MMNm to deviant phonemes and chords (*y* axis points to nasion, *z* axis toward the top of the head). (The error bars indicate the standard errors of the mean.) The ECD loci for monaural conditions include only the P1m and MMNm ECD loci modelled for contralateral stimulation.

tients with anterior lesions saving the temporal lobe displayed an MMN to a phonetic change (Aaltonen *et al.*, 1993). This further confirms the importance of the posterior areas of the left temporal lobe in processing phonetic information even at the preattentive level.

Moreover, the present data indicate that while in both hemispheres the MMNm source for the phoneme change was superior to that for the chord change, the P1m source location did not differ between the chords and phonemes (Fig. 3). This dissociation suggests that while the earlier processing stages of auditory information (as reflected by P1m) are independent of the stimulus content there are spatially distinct neuronal populations for representing the phonetic and musical stimuli (as reflected by MMNm).

Previous evidence has confirmed the tonotopical organization of the auditory cortex (Lauter *et al.*, 1985; Pantev *et al.*, 1995; Romani *et al.*, 1982; Tiitinen *et al.*, 1993; Wessinger *et al.*, 1997; Yamamoto *et al.*, 1992). In addition, it has been shown that a frequency change within spectrally complex sounds like chords is processed by a neuronal population spatially distinct from that processing a frequency change within pure sinusoidal tones (Alho *et al.*, 1996). The present data extend these results. Since the present stimuli were matched in complexity and also the frequency change in both conditions was of equal magnitude, the encountered difference in MMNm source location between phonetic and musical stimuli cannot be accounted for by physical stimulus differences. Instead, the data reveal that even preattentive neuronal processing of auditory information can be influenced by informational stimulus content.

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REFERENCES

Aaltonen, O., Tuomainen, J., Laine, M., and Niemi, P. 1993. Cortical differences in tonal versus vowel processing as revealed by an ERP component called mismatch negativity (MMN). *Brain Language* **44:**139–152.

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

Alku, P. 1992. Glottal wave analysis with pitch synchronous iterative adaptive inverse filtering. *Speech Commun.* **11:**109–118.

Auzou, P., Eustache, F., Etevenon, P., Platel, H., Rioux, P., Lambert, J., Lechevalier, B., Zarifian, E., and Baron, J. C. 1995. Topographic EEG activations during timbre and pitch discrimination tasks using musical sounds. *Neuropsychologia* **33:**25–37.

Benton, A. L. 1977. The Amusias. In *Music and the Brain* (M. Critchley and R. A. Henson, Eds.), pp. 378–397. Camelot, Southampton.

Bever, T. G., and Chiarello, R. J. 1974. Cerebral dominance in musicians and nonmusicians. *Science* **185:**537–539.

Binder, J. R., Rao, S. M., Hammeke, T. A., Frost, J. A., Bandettini, P. A., Jesmanowicz, A., and Hyde, J. S. 1995. Lateralized human brain language systems demonstrated by task subtraction functional magnetic resonance imaging. *Arch. Neurol.* **52:**593–601.

Buser, P., and Imbert, M. 1992. Audition. MIT Press, Cambridge, MA.

Diesch, E., and Luce, T. 1997. Magnetic fields elicited by tones and vowel formants reveal tonotopy and nonlinear summation of cortical activation. *Psychophysiology* **34:**501–510.

Gordon, H. W. 1970. Hemispheric asymmetries in the perception of musical chords. *Cortex* **6:**387–398.

Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., and Lounasmaa, O. V. 1993. Magnetoencephalography—Theory, instrumentation, and applications to noninvasive studies of the working human brain. *Rev. Mod. Phys.* **65:**413–497.

Hirskowitz, M., Earle, J., and Paley, B. 1978. EEG alpha asymmetry in musicians and nonmusicians: A study of hemispheric specialization. *Neuropsychologia* **16:**125–128.

Kuriki, S., and Murase, M. 1989. Neuromagnetic study of the auditory responses in right and left hemispheres of the human brain evoked by pure tones and speech sounds. *Exp. Brain Res.* **77:**127–134.

Kuriki, S., Okita, Y., and Hirata, Y. 1995. Source analysis of magnetic field responses from the human auditory cortex elicited by short speech sounds. *Exp. Brain Res.* **104:**144–152.

Langner, G., Sams, M., Heil, P., and Schulze, H. 1998. Frequency and periodicity are represented in orthogonal maps in the human auditory cortex: Evidence from magnetoencephalography. *J. Comp. Physiol.* A **181:**665–676.

Lauter, J. L., Herscovitch, P., Formby, C., and Raichle, M. E. 1985. Tonotopic organization in human auditory cortex revealed by positron emission tomography. *Hear. Res.* **20:**199–205.

Liégeois-Chauvel, C., Musolino, A., Barier, J. M., Marquis, P., and Chauvel, P. 1994. Evoked potentials recorded from the auditory cortex in man: Evaluation and topography of the middle latency hypothesis. *Electroencephal. Clin. Neurophysiol.* **92:**204–214.

Mäkelä, J. P., Hämäläinen, M., Hari, R., and McEvoy, L. 1994. Whole-head mapping of middle-latency auditory magnetic fields. *Electroencephal. Clin. Neurophysiol.* **92:**414–421.

Mazoyer, B. M., Tzourio, N., Frak, V., Syrota, A., Murayama, N., Levrier, O., Salamon, G., Dehaene, S., Cohen, L., and Mehler, J. 1993. The cortical representation of speech. *J. Cogn. Neurosci.* **5:**467–479.

Mazziotta, J. C., Phelps, M. E., Carson, R. E., and Kuhl, D. E. 1982. Tomographic mapping of human cerebral metabolism: Auditory stimulation. *Neurology* **32:**921–937.

Näätänen, R. 1992. *Attention and Brain Function.* Lawrence Erlbaum, Hillsdale, NJ.

Näätänen, R., Lehtokoski, A., Lennes, M., Cheour, M., Huotilainen, M., Iivonen, A., Vainio, M., Alku, P., Ilmoniemi, R. J., Luuk, A., Allik, J., Sinkkonen, J., and Alho, K. 1997. Language-specific phoneme representations revealed by electric and magnetic brain responses. *Nature* **385:**432–434.

Nicholls, M. E. R. 1996. Temporal processing asymmetries between the cerebral hemispheres: Evidence and implications. *Laterality* **1:**97–137.

Pantev, C., Hoke, M., Lütkenhöner, B., and Lehnertz, K. 1989. Tonotopic organization of the auditory cortex: Pitch versus frequency representation. *Science* **246:**486–488.

Pantev, C., Bertrand, O., Eulitz, C., Verkindt, C., Hampson, S., Schuirer, G., and Elbert, T. 1995. Specific tonotopic organizations of different areas of the human auditory cortex revealed by simultaneous magnetic and electric recordings. *Electroencephal. Clin. Neurophysiol.* **94:**26–40.

Paquette, C., Bourassa, M., and Peretz, I. 1996. Left ear advantage in pitch perception of complex tones without energy at the fundamental frequency. *Neuropsychologia* **34:**153–157.

Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., and Raichle, M. E. 1988. Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* **331:**585–589.

Pickles, J. O. 1988. *An Introduction to the Physiology of Hearing.* Academic Press, London.

Rinne, T., Alho, K., Alku, P., Sinkkonen, J., Virtanen, J., Bertrand, O., Holi, M., Tervaniemi, M., and Näätänen, R. 1997. Hemispheric asymmetry of cortical activation as reflected by the mismatch negativity reveals when a sound is processed as speech. *Soc. Neurosci. Abstr.* **23:**415:9.

Romani, G. L., Williamson, S. J., and Kaufman, L. 1982. Tonotopic organization of the human auditory cortex. *Science* **216:**1339–1340.

Sidtis, J. J. 1984. Music, pitch perception, and the mechanisms of cortical hearing. In *Handbook of Cognitive Neuroscience* (M. S. Gazzaniga, Ed.), pp. 92–112. Plenum, New York.

Tiitinen, H., Alho, K., Huotilainen, M., Ilmoniemi, R. J., Simola, J., and Näätänen, R. 1993. Tonotopic auditory cortex and the magnetoencephalographic (MEG) equivalent of the mismatch negativity. *Psychophysiology* **30:**537–540.

Wernicke, C. 1874. Der Aphasische Symptomencomplex: Eine Psychologische Studie auf anatomischer Basis. English translation in Wernicke's Works on Aphasia. *A Sourcebook and Review* (G. H. Eggert, Ed.), Mouton Publishers, The Hague, 1977.

Wessinger, C. M., Buonocore, M. H., Kussmail, C. L., and Mangun, G. R. 1997. Tonotopy in human auditory cortex examined with functional magnetic resonance imaging. *Human Brain Mapp.* **5:**18–25.

Yamamoto, T., Uemura, T., and Llinas, R. 1992. Tonotopic organization of human auditory cortex revealed by multi-channel SQUID system. *Acta Otolaryngol.* **112:**210–214.

Zatorre, R. J., Evans, A. C., Meyer, E., and Gjedde, A. 1992. Lateralization of phonetic and pitch discrimination in speech processing. *Science* **256:**846–849.