Neural correlates of auditory sensory memory and automatic change detection

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An auditory event-related potential component, the mismatch neg-ativity (MMN), reflects automatic change detection and its prerequisite, sensory memory. This study examined the neural correlates of automatic change detection using BOLD fMRI and two rates of presentation previously shown to induce either a large or no MMN. A boxcar block design was employed in two functional scans, each performed twice. A block consisting of 1000-Hz standards (S) alternated with one consisting of 1000-Hz standards and 2000-Hz infrequent deviants (S + D). Presentation rate was either 150 or 2400 ms. Fourteen participants were instructed to ignore all auditory stimulation and concentrate on a film (no audio) by reading subtitles. Data analysis used SPM99 and random effects approach. Cluster statistics ($P < 0.05$, corrected) were employed at a height threshold of $P < 0.001$. At the short ISI, there was a significant BOLD response in the right superior temporal gyrus (STG), the left insula, and the left STG (including parts of primary auditory cortex). There were no supra-threshold clusters at the long rate, with S + D blocks inducing no greater activity than S blocks. These results support the hypothesis that the automatic detection of auditory change occurs in the STG bilaterally and relies on the maintenance of sensory memory traces.
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Introduction

Auditory sensory (echoic) memory represents the initial record-ing of auditory information into the memory system. Its properties include rapid storage, brief duration (2–3 s), and detailed encoding of physical stimulus characteristics (e.g., Cowan, 1995; Darwin et al., 1972; Neisser, 1967). A paradigm useful in studying sensory memory is the so-called "oddball" task, in which a repeating signal (the "standard") is replaced periodically by an infrequent deviant (the "oddball"). Auditory event-related potential (ERP) studies indicate that oddballs reliably elicit a negative potential (relative to standards) approximately 100–300 ms after stimulus onset, even though subjects are instructed to ignore the auditory stimuli while engaged in a primary task, such as playing a video game or reading a book (Näätänen, 1990, 1992). This negative ERP component, called the mismatch negativity (MMN) response, may reflect the output of an automatic change-detection system. The evolutionary significance of such a system is its ability to monitor the environment for significant events, independent of conscious awareness or directed attention (e.g., detecting an alarm in a noisy environment).

Operation of the change-detection system, as reflected in the MMN, depends on how efficiently neuronal traces to deviant stimuli are compared with traces to the uniform stream of standard stimuli. In fact, the MMN will not be elicited unless the neuronal representation of the standards still exists at the moment when the deviant occurs (Winkler and Näätänen, 1995). Thus, an active sensory memory trace of standards is a prerequisite for activating the change detection mechanism underlying the MMN.

Recent electrophysiological research by Sabri and Campbell (2001) revealed that the MMN amplitude increased monotonically with the rate of stimulus presentation, even when the probability of a deviant occurring in time was held constant (e.g., one deviant on average every 9 s). In fact, at the slowest rate (i.e., 2.4 s), the negative wave was absent statistically (see also Alain et al., 1994). One interpretation is that faster rates yield stronger memory traces, probably because frequent repetitions lead to better encoding within the time-limited sensory memory buffer.

The anatomic basis of sensory memory remains largely un-known, as does the degree to which anatomic loci are shared between sensory systems. ERP (dipole-source modeling) and MEG recordings hint that echoic storage is located bilaterally on the supratemporal planes of the auditory cortex (e.g., Alho, 1995; Levänen et al., 1996; Scherg et al., 1989). However, the detection of acoustic change also may involve parietal and frontal regions (Giard et al., 1990; Levänen et al., 1996). Indeed, some researchers report an attenuated MMN response in the ipsilesional auditory cortex of patients with frontal lobe damage (Alho et al., 1994). Others report MMN attenuation contralaterally in patients with unilateral temporal–parietal lesions (Alain et al., 1998). Yet still

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others report no effects of temporal–parietal or inferior–parietal lesions on the MMN response (Woods et al., 1993).

Recent fMRI studies of the cortical network underlying change detection also have identified regions of sensory and nonsensory processing. Activation from multimodal change (i.e., auditory, visual, tactile) has been found in the right temporal–parietal junction (TPJ), inferior frontal gyrus (IFG), insula, left cingulate, and supplemental motor areas (e.g., Downar et al., 2000). When employing the passive versions of the auditory oddball paradigm (deviants were either ignored or did not require a response), activation has been localized bilaterally in the transverse/superior temporal gyri (TTG/STG; Celsis et al., 1999; Downar et al., 2000; Opitz et al., 1999, 2002), as well as in the right IFG (Opitz et al., 2002). Similarly, a recent PET study found that auditory change increased regional cerebral blood flow in the left and right STG, right ST sulcus, and left IFG (Müller et al., 2002).

In directly comparing the coordinates of activation reported in each of the fMRI studies of passive change detection, we found only a single anatomical locus of consensual agreement: right STG. The studies also commonly find activation in left STG, though here the coordinates vary. Finally, the insular and frontal cortices have been reported across several studies (Linden et al., 1999; Opitz et al., 2002).

In every previous neuroimaging study of change detection, the rate of stimulus presentation was *fixed*. Although several neuro-imaging studies have manipulated rates of stimulus presentation (e.g., of speech stimuli, words, or visual stimuli; see Binder et al., 1994; Fox and Raichle, 1985; Price et al., 1992), none investigated the automatic change detection response. Thus, to the best of our knowledge, our study is the first to investigate the effects of stimulus rate on passive change detection using fMRI. The importance of manipulating rate is to ensure that activation to automatic change detection emerges from sensory memory per se. Although extant studies using fixed rates have shown cortical responses to stimulus change, it is still possible that the obtained activation persisted outside the short inter-stimulus interval (ISI) and, hence, independently of the sensory memory system that underlies it. Should the response persist with longer intervals, it could not be attributed to sensory memory. Only by manipulating the rate of presentation can one confidently examine the neural correlates of echoic (sensory) memory and change detection. That is the purpose of the current study.

The current study employed two ISIs (short, long) proven to induce either a large MMN or, at the other extreme, no MMN. If the deviance-related activation in auditory cortex truly represents sensory memory, it should be reduced or eliminated at the long ISI (where no MMN is expected). We therefore hypothesized that: (a) compared with standards alone, Standards + Deviants would induce significant activation in the STG at the faster ISI, and (b) the same comparison at the longer ISI would not evoke significant activation in the STG. We also were interested in determining whether either ISI would evoke prefrontal activation.

Materials and methods

Subjects

Fourteen healthy right-handed volunteers (7 women; mean age = 27, SD = 4.0 years; education = 17.6 years, SD = 3.5) participated in the experiment. All subjects gave Institutional Review Board-approved, written informed consent. All were screened by self-report for head injury with loss of consciousness, other neurologic disorders that could affect cerebral function, and Axis-I psychiatric disorders.

Stimuli

Stimuli consisted of pure sine-wave tones of repetitive 1000 Hz (standards) and infrequent 2000 Hz (deviants) at a sound pressure level of ∼95 dB/SPL, each 100 ms in duration (including 10-ms rise and 10-ms fall time). Auditory stimuli were delivered binaurally via plastic sound conduction tubes threaded in foam ear tips, inside non-ferrous air-conducting headphones. Tone presentation was controlled by a personal computer running E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA) and a pneumatic-based audio system (Avotec, Jensen Beach, FL). The movie was displayed through high-resolution, fiber optic goggles (Avotec, Jensen Beach, FL) mounted on the head coil, just above the subjects' eyes.

Procedure

A boxcar block design was employed in two functional scanning sessions, each session performed twice. In all sessions, a block consisting of standards (S block) alternated with one consisting of standards and infrequent deviants (S + D block). The ISI was either 150 ms (short) or 2400 ms (long) throughout a session. Thus, differential activation between blocks in a given session would not be due to differences in stimulus presentation rate (see Rees et al., 1997). Each block lasted 45 s, with five off-states and four on-states for all tasks (see Fig. 1). When the ISI was short, the S blocks comprised 180 low-pitch tones and the S + D blocks comprised 175 low-pitch standards and 5 high-pitch, deviant tones. When the ISI was long, the S blocks comprised 18 low-pitch tones and the S + D blocks comprised 13 low-pitch standards and 5 high-pitch, deviant tones.

In both ISI conditions, temporal probability (i.e., the frequency of deviant occurrence in time) was held constant: Each of the five deviants in both ISI conditions occurred once every 9 s on average. Previous ERP research on the effects of conditional (sequential) and temporal probability has underscored the importance of controlling temporal probability in manipulations of stimulus rate (Sabri and Campbell, 2001). Note that experimenters can hold either sequential probability or temporal probability constant across tasks, but not both simultaneously.

Within each S + D block, the order of stimuli was randomized with the restriction that a minimum of two standards was interposed between deviants. The order of tasks was randomized across subjects. Subjects were instructed to ignore all auditory stimulation (tones and scanner noise) and to concentrate on a film (no audio) by reading the subtitles and preparing to answer yes/no questions after each scanning session. Subjects responded to the question by wiggling the right toe for 'yes' and left toe for 'no' following each scanning session.

Image acquisition

Functional images were acquired using the Gradient Echo EPI-BOLD pulse sequence on a 1.5T Signa GE LX Horizon scanner (Waukesha, WI). Functional imaging sessions comprised 196 images, acquired during each of four, 441 s sessions. Sixteen 8-
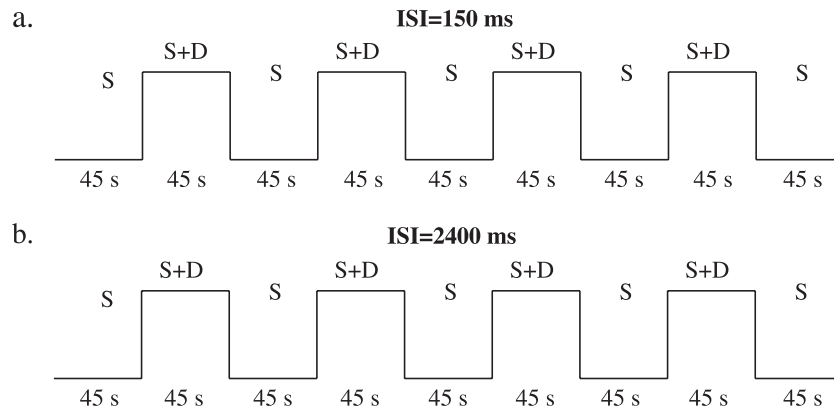
a.

ISI=150 ms

Fig. 1. Schematic illustrations of the temporal order for the oddball tasks. S = standard, S + D = standard + deviant. During the two sessions, five 'S' were alternated with four 'S + D' blocks, interstimulus interval (ISI) was either short (150 ms; panel a) or long (2400 ms; panel b). All blocks were 45 s in duration.
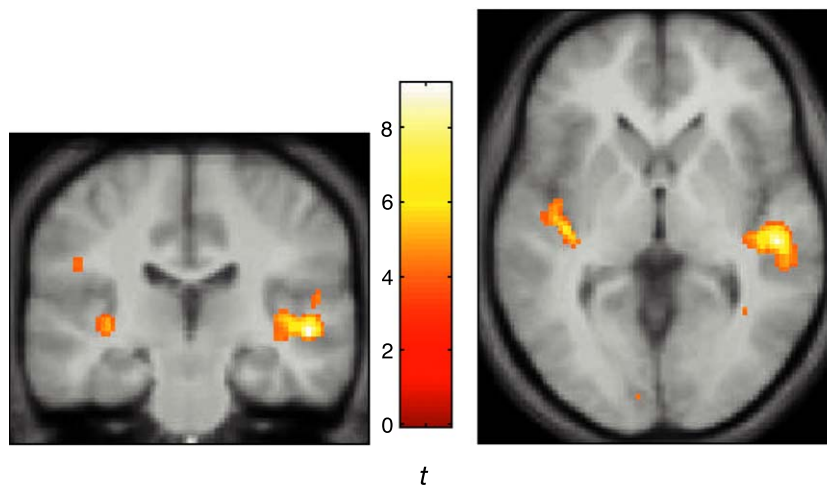

Fig. 2. Bilateral auditory cortical system activation superimposed on an averaged anatomical image in the short SIS condition (S + D > S contrast). Image threshold was set at $P < 0.001$, uncorrected. Right = Right.
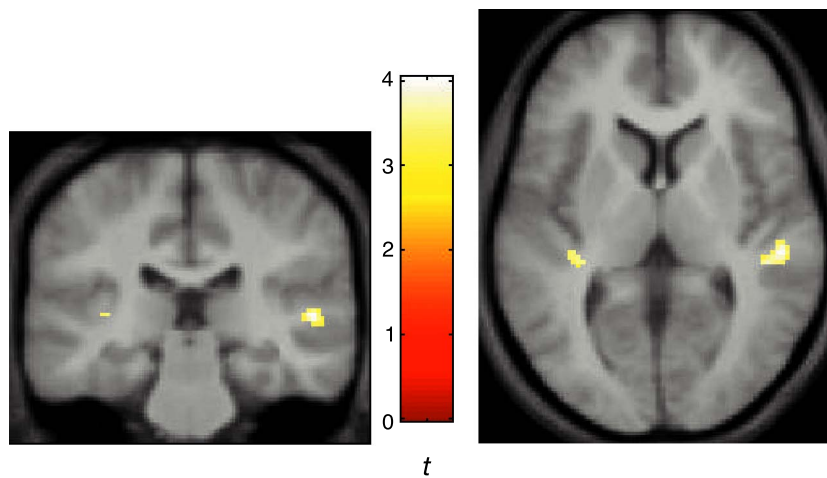

Fig. 3. Right and left STG in a contrast reflecting the comparison between the short and long ISI conditions as masked by the activation results in Fig. 2. Image threshold was set at $P < 0.005$, uncorrected. Right = Right.

mm-thick axial slices with no interslice gap were required to image the whole brain, repetition time/echo time (TR/TE) = 2.25 s/50 ms, flip angle (FA) = 90°, field-of-view (FOV) = 24 × 24 cm, matrix 64 × 64. High-resolution, heavily T1-weighted anatomic images were acquired for anatomic comparison (124 contiguous axial slices, 3D Spoiled-Grass sequence (SPGR), slice thickness 1.2 mm, TR/TE = 35/8 ms, FA = 30°, FOV = 24 × 24 cm, matrix 256 × 128). Subjects were fitted to an attached bite-bar using dental impression material and a head–neck pad to minimize head motion.

Image processing and data analysis

SPM99 (Wellcome Department of Cognitive Neurology, University College, London, UK) was used for data analysis. EP images were reconstructed using an 8.4 cm^{-1}/cycle Hamming window spatial smoothing filter to improve the signal-to-noise ratio (Lowe and Sorenson, 1997). Motion analysis (Woods et al., 1992) indicated maximum peak-to-peak displacement below 0.2 mm; thus no motion correction was applied. As statistical inference was derived from a random effects model (see below), neither temporal smoothing nor autoregression was applied. High-resolution 3D SPGR anatomic images of each subject were used to derive the parameters used for non-linear warping (7 × 8 × 7 basis functions, 12 iterations) of the subjects' images into stereotactic (Montreal Neurological Institute, MNI) space. These parameters then were used to transform the EPI images into the same coordinate space with an isotropic voxel size of 2 mm.

A random effects analytic strategy was employed by first using an fMRI model in SPM99 to summarize each subject's data into a single summary "contrast" image of a given condition by convolving the images with a standard boxcar reference function. A total of 180 images was analyzed after discarding the first 9 images to account for presaturation and the hemodynamic delay (Bandettini et al., 1993) and the last 7 images (to allow investigation of possible problems with the baseline MR signal). The contrast images were then analyzed with basic model *t* tests to assess the effect of a given condition. A one-sample *t* test was used to evaluate a given effect (set of contrast images) against a null hypothesis of zero. Contrasts consisted of images whose voxels reflected the effects of: [short ISI: S + D > S] and [long ISI: S + D > S]. To compare the short and long ISI sessions, a contrast image reflecting that comparison was written. The significance of this effect was then tested with a one-sample *t* test. Note that only the within-session contrasts explicitly controlled for the artifactual effects of overall rate of stimulus presentation on the magnitude of BOLD signals (see Rees et al., 1997). Cluster statistics ($P < 0.05$, corrected) were employed at a height threshold of $P < 0.001$.

The coordinates reported are MNI coordinates from the SPM output. To facilitate comparison to Rademacher et al.'s (2001) probability maps of primary auditory cortex (PAC) in Talairach space and to the Talairach atlas itself (Talairach and Tournoux, 1988), the MNI coordinates were converted to Talairach coordinates using the matlab function "mni2tal", (http://www.mrc-cbu.cam.ac.uk/imaging).

Regions of interest analyses

On the basis of theory and previous research (Alho, 1995; Celsis et al., 1999; Downar et al., 2000; Scherg et al., 1989; Levänen et al., 1996; Müller et al., 2002; Opitz et al., 1999, 2002), analysis concentrated on the bilateral STG in the short-greater-than-long contrast. The short ISI scan was used to "functionally" define bilateral STG region of interest by writing a binary image mask of the significant (threshold $P < 0.001$) activation in these areas (hence the inclusion of the insula). These regions were then searched for a comparison between the short and long ISI scans (threshold $P < 0.001$).

Results

Yes/no questions on visual task

Subjects' response accuracy was 96% (SD = 5%) across all sessions, indicating their compliance with the instructions.

Deviants (S + D) versus standards (S) contrasts

The short ISI task produced two significant clusters of activity in the left insula and left STG (-40, -18, -2), including parts of left PAC, and right STG, the latter of which was larger in spatial extent (52, -24, 0; Table 1, Fig. 2). The long ISI task produced no suprathreshold clusters of activity in any region of interest, nor in any other regions.

Short ISI > long ISI contrast

Within functionally defined STG (derived from activation of the short ISI task), the short ISI session produced significantly greater activation than did the long ISI in right STG (54, -28, 6; $P < 0.05$, corrected cluster significance). When the height threshold was reduced slightly ($P < 0.005$, uncorrected), two clusters in left STG were observed in -40, -18, -4 ($P < 0.05$ corrected cluster significance) and -34, -30, 6 ($P < 0.05$ corrected cluster signifi-

Table 1
Regions activated according to contrast within and between conditions

Contrast	MNI coordinates (x y z)	Region	z Value	Peak height (uncorrected)	Cluster size	Cluster probability (corrected)
(S + D)$_{short}$ > S$_{short}$	52, -24, 0	rSTG	5.02	$P < 0.001$	661	$P < 0.001$
	-40, -18, -2	lSTG/left insula	4.78	$P < 0.001$	184	$P < 0.005$
(S + D)$_{short}$ $-$ S$_{short}$ > (S + D)$_{long}$ $-$ S$_{long}$	54, -28, 6	rSTG	3.19	$P < 0.005$	74	$P < 0.001$
				$P < 0.001$	3	$P < 0.03$
	-40, -18, -4	lSTG/left insula	2.89	$P < 0.005$	15	$P < 0.02$
	-34, -30, 6		2.88	$P < 0.005$	10	$P < 0.04$

Note: Negative coordinates are left. S = standard, D = deviant. Short = 150 ms interstimulus interval (ISI), long = 2400 ms ISI. r = right, l = left. STG = superior temporal gyrus.

cance; see Table 1, Fig. 3). Similar results were obtained without the mask.

Discussion

The present study investigated the effects of long and short ISI on change detection of frequency deviants in the absence of directed auditory attention. During scanning and auditory stimulation, subjects focused on reading the subtitles of a film played with audio disabled. The change from standard tones to rare frequency deviant tones activated right STG, left STG (including parts of PAC), and left insula, but only when ISI was short. Deviant stimuli at the slower presentation rate did not elicit differential activation.

This is the first fMRI study to manipulate ISI in the passive oddball paradigm. As expected, STG and frontal regions were not recruited in contrasts where tones were presented relatively slowly. Similar parameters manipulated in an earlier ERP experiment revealed that the slow rate evoked overlapping responses to standard and deviant stimuli, yielding no MMN component in the difference waveform; in that study, only the fast rates evoked an MMN (Sabri and Campbell, 2001). The current study confirms these findings, and suggests that the anatomic locus for these effects is indeed right STG, left STG, and left insula. It thus appears that a slow rate of presentation promotes separate and similar processing of the standard and deviant such that their subtraction yields no significant signal difference. The lack of deviant-related activity when ISI was long demonstrates the crucial role of sensory memory in automatic change detection. Sensory memory is very brief; if not still active when the deviant occurs, an automatic change detection response will not be elicited.

One could attribute the lack of BOLD change detection response in this long ISI condition to the high sequential probability. However, in previous fMRI research, Opitz et al. (1999) established that a sequential probability very similar to the one selected in our study (33%) elicits a significant BOLD change detection response provided that the stimulus rate is shorter than in our long ISI condition (550 ms, compared with 2400 ms; see also Celsis et al. 1999). This research demonstrates that the higher sequential probability employed in our long ISI condition (28%) did not preclude the elicitation of a BOLD mismatch response. Rather, the mismatch response was eliminated by the slow presentation rate.

In accordance with earlier studies of automatic change response (Alho et al., 1998; Opitz et al., 1999, 2002; Scherg et al, 1989; Tervaniemi et al., 2000), deviant-related activation was right hemisphere dominant among all the different comparisons employed. Conversely, in studies employing phonemes or syllables, deviant automatic processing was lateralized to the left hemisphere (Tervaniemi et al., 2000). Activation in the left insula is consistent with previous reports relating this structure to a network of multimodal processing of sensory information (Downar et al., 2002; Linden et al., 1999). However, the deviant in the short ISI condition of this study did not elicit significant activity in any frontal regions. MRI, PET, and MEG studies (Giard et al., 1990; Levänen et al., 1996; Müller et al., 2002; Opitz et al., 2002) identified a second generator of the MMN in the prefrontal cortex. Yet the frontal generator's role in automatic change detection remains in debate, as the mismatch response to simple frequency deviance does not appear to be dependent on its activation.

The diverse experimental parameters and signal analyses employed in the various studies might account for the inconsistent results. For example, prefrontal activation, independent of the sensory MMN generator, may depend on the magnitude of deviance employed. Opitz et al. (2002), using spectrally rich tones in an event-related design, found that hemodynamic activation in the opercular part of the right IFG was modulated by deviance, but only for medium (30%) and large (100%) degrees of deviance. Another variable might be the spectral content of the stimuli. Activation in frontal regions was reported in response to complex sounds (Celsis et al., 1999; Downar et al., 2000) but not to pure sine waves, at least in fMRI (Celsis et al., 1999; Opitz et al., 1999; but see Müller et al., 2002).

Lesion studies appear to support the involvement of the frontal cortex in deviancy processing. Lesion of dorsolateral prefrontal cortex produced an attenuated response to the deviant stimuli and an enhanced N1 amplitude to standard stimuli resulting in MMN decrement compared with healthy controls (Alain et al., 1998; Alho et al., 1994). The N1 pattern suggests that frontal lesions do not affect auditory analysis in general but are more likely to affect discrimination processes, as the performance of frontal patients on an auditory discrimination task is slower and less accurate. In addition, the N2-P3a wave complex that is elicited following an attentional switch to a novel or salient auditory deviant is attenuated in frontal patients (see Friedman et al., 2001 for a review). One possibility consistent with those findings is that the prefrontal cortex serves as a secondary generator when attention switching occurs following involuntary detection of auditory irregularity between neural traces or following active discrimination (Escera et al., 1998; Giard et al., 1990; Näätänen, 1992). However, the precise role of the frontal cortex in deviancy processing and its interplay with the temporal cortices requires further investigation.

In summary, right STG, left STG, and left insula activations were present only at the shorter ISI condition, consistent with the implicated role of sensory memory in automatic change detection. Lack of such activation at the longer ISI suggests the fading of memory or context at this interval. The precise role of frontal cortex in signal change detection remains to be elucidated.

References

Alain, C., Woods, D.L., Ogawa, K.H., 1994. Brain indices of automatic pattern processing. NeuroReport 6, 140–144.

Alain, C., Woods, D.L., Knight, R.T., 1998. A distributed cortical network for auditory sensory memory in humans. Brain Res. 812, 23–37.

Alho, K., 1995. Cerebral generators of mismatch negativity (MMN) and its magnetic counterpart (MMNm) elicited by sound changes. Ear Hear. 16, 38–60.

Alho, K., Woods, D.L., Algazi, A., Knight, R.T., Näätänen, R., 1994. Lesions of frontal cortex diminish the auditory mismatch negativity. Electroencephalogr. Clin. Neurophysiol. 91, 353–362.

Alho, K., Winkler, I., Escera, C., Huotilainen, M., Virtanen, J., Jääskeläinen, I.P., Pekkonen, E., Ilmoniemi, R.J., 1998. Processing of novel sounds and frequency changes in the human auditory cortex: magnetoencephalographic recordings. Psychophysiology 35, 211–224.

Bandettini, P.A., Jesmanowicz, A., Wong, E.C., Hyde, J.S., 1993. Processing strategies for time-course data sets in functional MRI of the human brain. Magn. Reson. Med. 30, 161–173.

Binder, J.R., Rao, S.M., Hammeke, T.A., Frost, J.A., Bandettini, P.A., Hyde, J.S., 1994. Effects of stimulus rate on signal response during functional magnetic resonance imaging of auditory cortex. Cogn. Brain Res. 2, 31–38.

Celsis, P., Boulanouar, K., Doyon, B., Ranjeva, J.P., Berry, I., Nespoulous, J.L., Chollet, F., 1999. Differential fMRI responses in the left posterior superior temporal gyrus and left supramarginal gyrus to habituation and change detection in syllables and tones. NeuroImage 9, 135–144.

Cowan, N., 1995. Attention and Memory: An Integrated Framework. Oxford University Press.

Darwin, C.J., Turvey, M.T., Crowder, R.G., 1972. An auditory analogue of the Sperling partial report procedure: evidence for brief auditory storage. Cogn. Psychol. 3, 255–267.

Downar, J., Crawley, A.P., Mikulis, D.J., Davis, K.D., 2000. A multimodal cortical network for the detection of changes in the sensory environment. Nat. Neurosci. 3, 277–283.

Downar, J., Crawley, A.P., Mikulis, D.J., Davis, K.D., 2002. A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. J. Neurophysiol. 87, 615–620.

Escera, C., Alho, K., Winkler, I., Näätänen, R., 1998. Neural mechanisms of involuntary attention to acoustic novelty and change. J. Cogn. Neurosci. 10, 590–604.

Fox, P.T., Raichle, M.E., 1985. Stimulus rate determines regional brain blood flow in striate cortex. Ann. Neurol. 17, 303–305.

Friedman, D., Cycowicz, Y.M., Gaeta, H., 2001. The novelty P3: an event-related brain potential (ERP) sign of the brain's evaluation of novelty. Neurosci. Biobehav. Rev. 25, 355–373.

Giard, M.H., Perrin, F., Pernier, J., Bouchet, P., 1990. Brain generators implicated in processing of auditory stimulus deviance: a topographic event-related potential study. Psychophysiology 27, 627–640.

Levänen, S., Ahonen, A., Hari, R., McEvoy, L., Sams, M., 1996. Deviant auditory stimuli activate human left and right auditory cortex differently. Cereb. Cortex 98, 493–501.

Linden, D.E.J., Prvulovic, D., Formisano, E., Völlinger, M., Zanella, F.E., Goebel, R., Dierks, T., 1999. The functional neuroanatomy of target detection: an fMRI study of visual and auditory oddball tasks. Cereb. Cortex 9, 815–823.

Lowe, M.J., Sorenson, J.A., 1997. Spatially filtering functional magnetic resonance imaging data. Magn. Reson. Med. 37, 723–729.

Müller, B.W., Jüptner, M., Jentzen, W., Müller, S.P., 2002. Cortical activation to auditory mismatch elicited by frequency deviant and complex novel sounds: a PET study. NeuroImage 17, 231–239.

Näätänen, R., 1990. The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. Behav. Brain Sci. 13, 201–288.

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

Neisser, U., 1967. Cognitive Psychology. Appleton-Century-Crofts, New York, NY.

Opitz, B., Mecklinger, A., Von Cramon, D.Y., Kruggel, F., 1999. Combining electrophysiological and hemodynamic measures of the auditory oddball. Psychophysiology 36, 142–147.

Opitz, B., Rinne, T., Mecklinger, A., von Cramon, D.Y., Schröger, E., 2002. Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. NeuroImage 15, 167–174.

Price, C., Wise, R., Ramsay, S., Friston, K., Howard, D., Patterson, K., Frackowiak, R., 1992. Regional response differences within the human auditory cortex when listening to words. Neurosci. Lett. 146, 179–182.

Rademacher, J., Morosan, P., Schormann, T., Schleicher, A., Werner, C., 2001. Probabilistic mapping and volume measurement of human primary auditory cortex. NeuroImage 13, 669–683.

Rees, G., Howseman, A., Josephs, O., Frith, C.D., Friston, K.J., Frackowiak, R.S.J., Turner, R., 1997. Characterizing the relationship between BOLD contrast and regional cerebral blood flow measurements by varying the stimulus presentation rate. NeuroImage 6, 270–278.

Sabri, M., Campbell, K.B., 2001. Effects of sequential and temporal probability of deviant occurrence on mismatch negativity. Cogn. Brain Res. 12, 171–180.

Scherg, M., Vajsar, J., Picton, T.W., 1989. A source analysis of the late human auditory evoked potentials. J. Cogn. Neurosci. 1, 336–355.

Talairach, J., Tournoux, P., 1988. Co-Planar Stereotaxic Atlas of the Human Brain. Thieme, Stuttgart.

Tervaniemi, M., Medvedev, S.V., Alho, K., Pakhomov, S.V., Roudas, M.S., van Zuijen, T.L., Näätänen, R., 2000. Lateralized automatic auditory processing of phonetic versus musical information: a PET study. Hum. Brain Mapp. 10, 74–79.

Winkler, I., Näätänen, R., 1995. The effects of auditory backward masking on event-related brain potentials. In: Karmos, G., Csépe, V., Czigler, I., Molnar, M., Desmedt, J. (Eds.), Perspectives of ERP Research, EEG Suppl. 44. Elsevier, Amsterdam, pp. 185–189.

Woods, R.P., Cherry, S.R., Mazziotta, J.C., 1992. Rapid automated algorithm for aligning and reslicing PET images. J. Comput. Assist. Tomogr. 16, 620–633.

Woods, D.L., Knight, R.T., Scabini, D., 1993. Anatomical substrates of auditory selective attention: behavioral and electrophysiological effects of posterior association cortex lesions. Cogn. Brain Res. 1, 227–240.