Temporal integration of sequential auditory events: silent period in sound pattern activates human planum temporale

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Abstract

Temporal integration is a fundamental process that the brain carries out to construct coherent percepts from serial sensory events. This process critically depends on the formation of memory traces reconciling past with present events and is particularly important in the auditory domain where sensory information is received both serially and in parallel. It has been suggested that buffers for transient auditory memory traces reside in the auditory cortex. However, previous studies investigating "echoic memory" did not distinguish between brain response to novel auditory stimulus characteristics on the level of basic sound processing and a higher level involving matching of present with stored information. Here we used functional magnetic resonance imaging in combination with a regular pattern of sounds repeated every 100 ms and deviant interspersed stimuli of 100-ms duration, which were either brief presentations of louder sounds or brief periods of silence, to probe the formation of auditory memory traces. To avoid interaction with scanner noise, the auditory stimulation sequence was implemented into the image acquisition scheme. Compared to increased loudness events, silent periods produced specific neural activation in the right planum temporale and temporoparietal junction. Our findings suggest that this area posterior to the auditory cortex plays a critical role in integrating sequential auditory events and is involved in the formation of short-term auditory memory traces. This function of the planum temporale appears to be fundamental in the segregation of simultaneous sound sources.
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Introduction

In the auditory domain, where sensory signals are received both serially and in parallel, temporal integration (Bregman, 1990) and transient storage of pattern representations (Näätänen, 1990, 1992; Näätänen and Winkler, 1999) of discrete events are particularly important for deciphering information, the construction of perceptual units, and the detection of changes in the environment. Rare and unexpected events violating regular temporal patterns typi-

cally elicit an electrophysiological response peaking shortly after the irregularity. The generation of this mismatch response (Näätänen et al., 2001) is automatic, largely independent of attention, and is thought to reflect neural activity of brain circuits involved in transient auditory information storage (Tiitinen et al., 1994). Such memory traces ("echoic memory") play a key role in the assessment of the familiarity or novelty of a stimulus and thus represent a critical process in the cascade of working and long-term memory formation (Goldman-Rakic, 1995).

Electrophysiological studies in animals and humans suggest that mismatch responses to deviant sounds are generated by neural circuits located in the vicinity of the primary auditory cortex (Scherg et al., 1989; Javitt et al., 1996). This

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evidence is based on studies that used deviant auditory stimuli, which were—compared to the preceding stimuli—varied in intensity, duration, or pitch. However, by introducing a change in a stimulus characteristic, it is difficult to discern whether the mismatch responses arise from recruitment of stored information traces or whether they represent neural activity induced by the novel characteristics of the deviant stimulus. To make this distinction and to probe transient auditory memory traces, we used brief periods of silence as deviant events (by omitting single sound stimuli), which are known to produce characteristic electrophysiological mismatch or mismatch-like responses in the human brain (e.g., Sutton et al., 1967; Klinke et al., 1968; Simson et al., 1976; Joutsiniemi and Hari, 1989; Joutsiniemi et al., 1989; Nordby et al., 1994; Tervaniemi et al., 1994; Raij et al., 1997; Yabe et al., 1997, 1998, 2001; Hughes et al., 2001; Busse and Woldorff, 2003).

We hypothesized that the planum temporale plays a role in the formation of short-lived acoustic memory traces. This area comprising secondary and association auditory cortex posterior to Heschl's gyrus (Galaburda and Sanides, 1980; Rivier and Clarke, 1997; Westbury et al., 1999; Hackett et al., 2001) can be considered as a "computational hub," which carries out complex auditory processing operations that are mandatory for segregating spectrotemporal sound patterns and matching them with stored representations (Griffiths and Warren, 2002). For example, the perception of apparent auditory motion, which is a typical case of sensory task requiring temporal integration, produces circumscribed and obligatory neural activation in the planum temporale extending into the temporoparietal junction (Baumgart et al., 1999; Seifritz et al., 2002b; Warren et al., 2002). To address our hypothesis and identify the neural underpinnings of auditory memory traces in the human brain, we used blood oxygen level-dependent (BOLD) functional magnetic resonance imaging (fMRI). However, fast fMRI is inevitably associated with considerable background noise generated by the gradient switches, which produce spatially and temporally specific neural activation in the auditory cortex (Bandettini et al., 1998; Hall et al., 2000; Seifritz et al., 2002a). To avoid interference between scanner noise and auditory task, we developed an image acquisition scheme that allowed us to modify these sounds and to employ brief periods of silence or brief periods of increased loudness as deviant events interspersed within a pattern of regularly repeated sounds.

Materials and methods

Subjects

Eight healthy subjects (six men, two women) aged between 26 and 48 years participated in this study. All subjects except for one woman were right-handed. Informed consent was obtained from all subjects after approval by the local ethics committee.

Combined image acquisition and auditory stimulation

Data were acquired on a 1.5-T Symphony scanner equipped with a Sonata gradient system and a circularly polarized head coil (Siemens, Erlangen, Germany). For whole-brain structural volumes we used a T_1-weighted three-dimensional magnetization prepared rapid acquisition gradient echo sequence with a voxel size of 1 mm^3. The functional volumes (230 repetitions) were positioned parallel to the lateral sulcus and consisted of a gradient-recalled echoplanar imaging sequence with six image slices (pairs of functional and dummy images, see below) having a slice thickness of 5 mm and a volume repetition time of 1200 ms (echo time, 60 ms; flip angle, 60°; image and dummy slice acquisition times, 100 ms each; field of view, 200 × 200 mm^2; matrix, 64 × 64 pixels).

To bypass the interaction between experimental stimulation and background noise, which is inevitably associated with rapid gradient switches during fMRI data acquisition and which produces auditory cortex excitation per se, we designed an echoplanar imaging sequence consisting of alternating pairs with (1) functional image acquisitions with radiofrequency pulse-induced slice excitation and with (2) dummy images without radiofrequency excitation (Fig. 1). Pairing functional and dummy images allowed us to modulate the gradient pulses and the consequent sounds generated by the dummy scan without influencing the signal of the functional images.

The B_0 gradient switches during functional image acquisition produced sounds with a base frequency of 753 Hz and sound level of 98 dB lasting 82 ms. Design modifications (Bilecen et al., 1998) of the dummy image readout gradients allowed us to generate three different auditory stimulus modalities, (1) regular pattern of sounds (where gradients of the functional images and the dummy slices were identical: sound level, 98 dB; base frequency, 753 Hz; the sounds of 82-ms duration were interrupted by 18 ms of silence, which resulted in a 10 Hz amplitude modulated acoustic signal), (2) pattern of sounds with silent periods (by leaving out the gradient switches of one single dummy slice, 0 dB for 100 ms), or (3) pattern of sounds with periods of louder sound (by increasing the gradient amplitude of one single dummy slice, 113 dB, 753-Hz base frequency for 82 ms). The deviant stimuli generated by the modified dummy image B_0 gradient switches were alternately presented every 24 s. We used an alternating rather than a random pattern of stimulus presentation because mismatch negativity responses to deviant events are insensitive to the predictability of their occurrence (Scherg et al., 1989; Sussman et al., 1998; Rinne et al., 2001) and to avoid systematic time-related effects occurring throughout scan sessions. Subjects were equipped with bilateral headphones (Commander XG, Resonance Technology, Northridge, CA) that attenuated the scanner
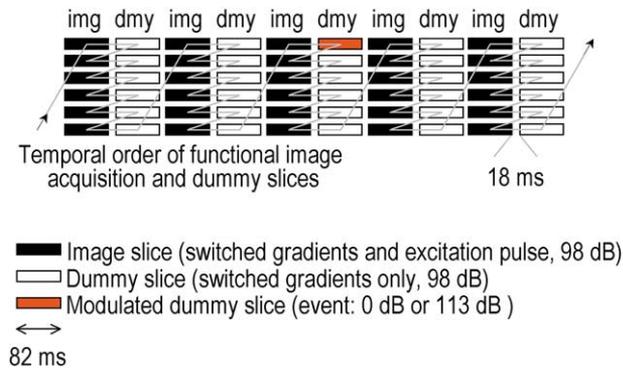
Fig. 1. Combined stimulation and image acquisition procedure. The B_0 gradient switches during both functional image and dummy slice acquisition produced a regular pattern of repetitive sounds (98-dB sound pressure level, 753-Hz base frequency, 82-ms duration, 18-ms interruption) with a 10-Hz amplitude modulation. The dummy images consisted of gradient switches only without slice excitation pulses. This allowed us to modify the dummy gradients without influencing the signal of the functional images (Bilecen et al., 1998) and to generate two types of deviant events, silence and louder sound. These deviant events were presented alternately every 24 s and were embedded into the regular sound pattern.

sounds by 30 dB and were instructed to listen to the stimuli with their eyes open, but not to react to them or to carry out any output task. Each trial (230 scans) lasted 276 s and was repeated two times in each subject within the same experimental session.

Data analysis

The first 20 functional scans were discarded to reach steady state in terms of both scanner-induced auditory ex-
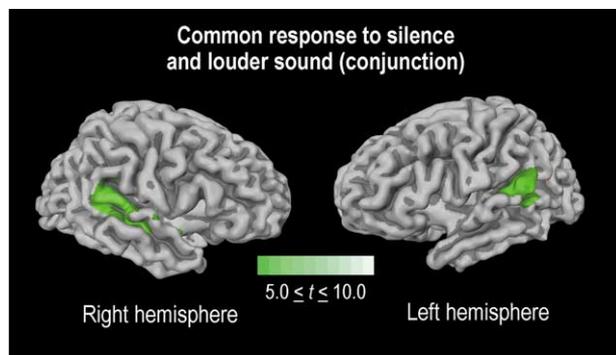

Fig. 2. Common brain response to brief periods of silence and increased loudness during the presentation of a regular pattern of repetitive sounds (cf. Fig. 1). A conjunction analysis (Price and Friston, 1997; Friston et al., 1999) revealed that the deviant stimuli induced common neural activity bilaterally in the superior temporal gyri and sulci covering posterior secondary and association auditory cortices bilaterally and partially the right Heschl's gyrus (lateral portion) and the right planum polare. This activity pattern, which was not specific for the type of event, represents the response to stimulus deviance (change detection). The activity pattern showed the following three local maxima expressed in *x/y/z* Talairach coordinates: left hemisphere, $-56/-35/13$ mm ($t_{3342} = 9.22$, $Z = 7.70$); right hemisphere, $48/-18/0$ mm ($t_{3342} = 8.27$, $Z = 7.42$), and $56/-33/11$ mm ($t_{3342} = 9.63$, $Z = 7.80$).
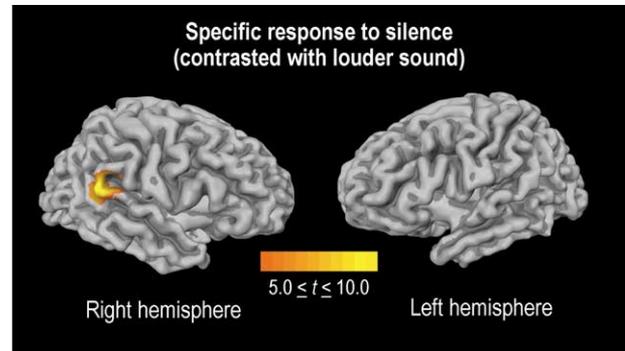

Fig. 3. Specific brain response to brief periods of silence as compared to brief periods of increased loudness during the presentation of a regular pattern of repetitive sounds (cf. Fig. 1). The general linear contrast (Friston et al., 1995) between the two deviant events revealed specific neural activation in the right planum temporale and its extensions to the right temporoparietal junction. Neural activation elicited by the silent event was found exclusively in the right hemisphere in a neural stream that was posteriorly directed relative to Heschl's gyrus with its local maximum (in *x/y/z* Talairach coordinates) at $58/-43/19$ mm ($t_{3342} = 6.84$, $Z = 6.73$). This response arising during the absence of a veridical stimulus represents neural activity related to auditory memory trace recruitment.

citation and longitudinal magnetization. Image analyses were carried out using Brainvoyager 4.6 (BrainInnovation, Maastricht, The Netherlands). The time series were corrected for slice acquisition time through linear interpolation, realigned with their corresponding T_1 volumes, warped into standard space, resampled into 3-mm isotropic voxels, motion-corrected using Levenberg-Marquart's least square fit for six spatial parameters, corrected voxelwise for linear drifts, and spatially smoothed using a 6-mm full-width at half-maximum gaussian kernel. Condition-specific functions were convolved with a double gamma function (Friston et al., 1998) to model the hemodynamic response behavior. Cortical areas responding to the deviant events (silence, louder sound) were identified by conjunction analyses to identify brain activation common to both stimulus types (Price and Friston, 1997; Friston et al., 1999) and by general linear contrasts to identify brain activation specific for one but not the other stimulus type of the time series in each image voxel (Friston et al., 1995). The conjunction analysis as implemented in Brainvoyager 4.6 computes three separate maps representing first the main effects of the two conditions and then the corresponding interaction. Subsequently, those regions that are significantly active in the two main effects maps but not active in the third map (interaction) survive the conjunction step. A conjunction map is produced by computing at each selected voxel a new statistical value as the minimum of the statistical values obtained from the first two maps (main effects). To account for interstudy signal differences in level and variance, the time series were *z*-transformed. The general linear model analysis and thus the Bonferroni correction have been performed over 16,623 voxels ($t_{3342} \geq 5.0$, $P \leq 0.01$).

Results and discussion

To specify the brain area showing neural response to both the silent period and the period with increased loudness, we used general linear model and conjunction analyses with the two stimulus types as explanatory variables. We found neural activity commonly elicited by both types of event, silence and louder sound, in the temporal cortex, including the planum temporale of both hemispheres (Fig. 2). This is consistent with findings from a previous fMRI study that also used design modifications of the image acquisition sequence (Mathiak et al., 2002). In the right hemisphere, activity included also the planum polare and the lateral portion of Heschl's gyrus. This common bilateral response extended posteriorly into the temporoparietal junction. Because violation of the preceding regular sound pattern was the common denominator of the two qualitatively opposite stimuli and because neural activation was not specific for the type of stimulus, bilateral activity in these primary, secondary, and association auditory cortices reflects a general response to change (Linden et al., 1999) or sequential transition (Downar et al., 2000). To separate this novelty response from activity related to memory trace recruitment, we directly compared the pattern of neural activation elicited by silence with the neural activation pattern elicited by increased loudness. By contrasting the two stimulus types, we found that silence compared to increased loudness produced specific activity that was confined to the right planum temporale and posteriorly to the temporoparietal junction (Fig. 3). This response pattern was present in the right but not in the left hemisphere at the probability level used in our analysis; in addition, lateralization to the right hemisphere was preserved even when we lowered the statistical threshold to nonsignificant levels. The inverse contrast, that is, increased loudness compared with silence, did not produce significant BOLD responses.

A brief period of silence occurring during a regular pattern of rapidly repeated sounds produced circumscribed neural activation in the right planum temporale and temporoparietal junction. The selective and specific response to violation of a preceding temporal sound pattern in combination with the absence of a veridical sound stimulus suggests that the neural activity reflects processes associated with the recruitment of auditory memory traces. However, it is important to emphasize that our findings are based on an acoustic event sequence with a regular interstimulus interval of 100 ms. This interval falls within the boundaries of the so-called "temporal window of integration" having an upper limit of approximately 200 ms (Näätänen, 1992), during which sequentially presented discrete auditory events tend to be associated, or integrated, to a coherent perceptual unit (Cowan, 1984). Omitted stimuli that are expected to occur within this time window typically elicit electrophysiological mismatch responses in areas of the temporal lobe (Joutsiniemi et al., 1989; Tervaniemi et al., 1994; Yabe et al., 1997, 1998, 2001). Spatially more confined, intracortical electro-

encephalographic recordings in patients with different kinds of brain lesions yielded, consistent with our data, omission-specific neural responses in the planum temporale (Hughes et al., 2001). Notably, deviant omissions during regular sequences with interstimulus intervals longer than this 200-ms window can elicit mismatch negativity-like responses as well (e.g., Sutton et al., 1967; Klinke et al., 1968; Simson et al., 1976; Joutsiniemi and Hari, 1989; Nordby et al., 1994; Raij et al., 1997; Busse and Woldorff, 2003); however, there is debate as to whether these responses reflect the same or different underlying cognitive and neural processes (Ross et al., 2002).

The intertrial variability of event-related hemodynamic responses detected in fMRI (Duann et al., 2002; Henson et al., 2002) do not allow us to define the exact point in time at which neural activity was initiated. For instance, we cannot directly determine whether the BOLD response we observed was initiated at the offset of the last regular auditory event before the silent period, at the time the next event would be expected (that is, about at the midpoint of the silent period), or at the initiation of the acoustic event following the silent period. However, the latter possibility is unlikely considering that auditory cortex activity elicited with similar stimuli presented after a long period of silence is bilateral rather than confined to the right planum temporale (Seifritz et al., 2002a). On a finer time scale than that provided by fMRI, magnetoencephalographic work demonstrates distinct differences between the response to silence (initiated at the predicted time of the omitted stimulus) and the response to the first tone after the omission (Raij et al., 1997).

The lateralization of neural activity in our data appears to be consistent with magnetoencephalographic and positron emission tomographic studies demonstrating that stimulus quality can determine the preferred hemisphere of response. Tasks addressing the temporal processing of tonal sound patterns tend to elicit electrical and hemodynamic mismatch responses in the right temporal cortex, whereas tasks addressing the processing of language-related sound patterns elicit mismatch responses in the left temporal cortex (Näätänen et al., 1997; Tervaniemi et al., 2000). The localization of neural response in the right planum temporale and the temporoparietal junction is furthermore consistent with electrophysiological and hemodynamic changes observed during the early phases of electrical mismatch responses to veridical nonverbal auditory stimuli (Paavilainen et al., 1991; Opitz et al., 2002).

Spatially, our findings are reminiscent of the brain areas involved in the perception of auditory space and motion (Baumgart et al., 1999; Tian et al., 2001; Zatorre and Penhune, 2001; Seifritz et al., 2002b; Warren et al., 2002). Auditory motion perception, for which the planum temporale plays a particularly important role, may tentatively be considered to depend on spatiotemporal processes integrating auditory signal changes over time. In addition, some evidence also suggests that the right auditory cortex is

specifically involved in the directional analysis of sound pattern changes including pitch (Johnsrude et al., 2000) and loudness (Seifritz et al., 2002b). Interestingly, this is true even though the left auditory cortex appears to be equipped with higher temporal resolution capability, an ability that is thought to be related with the demands of language processing (Zatorre and Belin, 2001). In somewhat speculative analogy to other sensory systems, our findings could represent recurrent neural feedback loops between association, secondary and primary cortex (Pascual-Leone and Walsh, 2001), which subserve an ongoing updating between stored and present sensory information (Egorov et al., 2002). These loops also certainly involve more distant brain areas, which were not examined in the present study (Goldman-Rakic, 1995). However, our findings specifically identify a novel functional dimension associated with the planum temporale and its posterior extensions into the temporoparietal junction. The preattentive memory trace-dependent temporal integration of sequential sound events represents a fundamental yet missing aspect to the emerging concepts about the pivotal role of this brain area in auditory information processing (Griffiths and Warren, 2002). Thus, our data suggest that the planum temporale plays a role in using stored representations that appear to be fundamental in the segregation of simultaneous sound sources.

Acknowledgments

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