Human auditory cortical processing of transitions between 'order' and 'disorder'

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1 Introduction

Sensitivity to changes in sound is important to auditory scene analysis and detection of the appearance of new objects in the environment. In this paper we describe two experiments that used Magnetoencephalography (MEG) to investigate the temporal dynamics of auditory cortical responses to changes in ongoing stimuli. The experiments used very different stimuli (dichotic vs. diotic, noiselike vs. tonal, stationary vs. dynamic), but shared the abstract characteristic that they both involved a transition from a state of order to disorder, or vice-versa (Figure 1). In one experiment (Chait, Poeppel, de Cheveigne and Simon 2005) we studied changes in the interaural correlation (IAC) of wide-band noise. Stimuli consisted of interaurally correlated noise (identical noise signals played to the two ears) that changed into uncorrelated noise (different noise signals at the two ears) or vice versa. The stimuli of the second experiment were designed to mimic the abstract properties of those in the IAC experiment, while changing the acoustic properties completely. Signals consisted of a constant tone that changed into a sequence of random tone pips, or vice versa. In both experiments, magnetic responses were gathered while subjects attended to an auditory task unrelated to the dimension along which the stimuli varied. The responses are thus presumed to reflect pre-attentive 'bottom-up' mechanisms, processing aspects of sound that the subject does not attend to consciously.

We show that early auditory cortical responses are remarkably similar between experiments. For both experiments, the response pattern differed radically between transitions from order to disorder and vice-versa. We interpret this result as possibly reflecting the different requirements of the process that estimates the regularity of the stimulus (interaural correlation vs. decorrelation, constant tone vs.

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random pip sequence) according to the direction of the change. The data shed light on the heuristics with which auditory cortex samples, represents, and detects changes in the environment, including those that are not the immediate focus of attention.
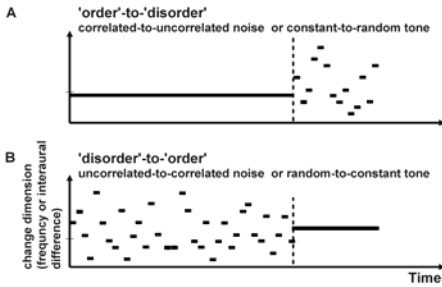

Figure 1: Schematic representation of the abstract similarity between the stimuli used in the two experiments. In the IAC experiment, the dimension of change (Y axis) is interaural difference. Correlated noise is hypothesized (Durlach 1963) to be represented as a constant 'zero' value, whereas uncorrelated noise is represented as a randomly fluctuating value. The size of the black segments symbolizes the temporal resolution of binaural processing. In the tone experiment, the dimension of change is frequency. Pip size (black segments) is 30ms.

2 Materials and Methods

Methods are described in full in Chait et al (2005).

Subjects: 18 and 24, right handed, paid subjects gave written informed consent to participate in the IAC and tone experiments, respectively. We also conducted behavioral experiments with the same subjects and stimuli, the results of which are reported elsewhere (Chait et al 2005; Chait et al in preparation).

Stimuli: The signals in the IAC experiment were 1100 ms-long wide-band noise bursts, consisting of an initial 800 ms-long segment (reference correlation) that was either interaurally correlated (IAC = 1) or interaurally uncorrelated (IAC = 0), followed by a 300 ms segment with one of six fixed values of IAC: 1.0, 0.8, 0.6, 0.4, 0.2, 0.0. The purpose of the relatively long initial segment was to ensure that responses to change in IAC do not overlap with those associated with stimulus onset. Stimuli were ramped on and off with 15ms cosine-squared ramps and presented in random order with an inter-stimulus interval that was varied randomly between 600 and 1400 ms.

The signals in the tone experiment were 1440 ms long, consisting of an initial 840 ms pre-transition segment (either random or constant), immediately followed by a 600 ms post-transition segment (either random or constant). Controls were 1440ms random or constant throughout. Random sequences contained successive tone pips of a random frequency. We used 3 pip durations (15, 30 and 60 ms) which were presented by blocks. Frequencies were drawn from 20 frequency values equally spaced on a log scale between 222-2000 Hz. Tone and pip onsets and offsets were ramped with 3ms cosine-squared ramps. Presentation order was randomized with an inter-stimulus interval between 600-1400 ms.

The stimulus set also included a proportion (25-33%) of target stimuli (not analyzed), which subjects were required to rapidly respond to. These stimuli served to keep the listeners alert and attentive but did not involve IAC or tone-change processing.

Neuromagnetic recording and analysis: The magnetic signals were recorded using a 160-channel, whole-head axial gradiometer system (KIT, Kanazawa, Japan). The 20 strongest channels over the temporal regions of the head of each subject (5 sinks and 5 sources in each hemisphere) were determined in a pre-experiment (see Chait et al, 2005).

Two measures of dynamics of cortical processing are reported: the amplitude time course (increases and decreases in activation) as reflected in the root mean square (RMS) of the selected channels, and the accompanying spatial distributions of the magnetic field (contour plots) at certain times post onset. For illustration purposes, we plot the RMS derived from the grand-average (average over all subjects for each of the 160 channels) but the statistical analysis is always performed on a subject-by-subject, hemisphere by hemisphere, basis, using the RMS values of the 10 channels chosen for each subject in each hemisphere.

1500 ms epochs (including 200 ms pre onset) were created for each of the stimulus conditions. Approximately 100 epochs of each condition were averaged, low-pass filtered at 30 Hz, and base-line corrected to the pre-onset interval. The consistency, across subjects, of peaks and magnetic field distributions was assessed automatically as described in Chait et al (2005).

3 IAC experiment results

Clear transition responses were recorded from auditory cortex even though listeners performed a task that is irrelevant to IAC change. In Chait et al (2005) we show that this pre-attentive cortical sensitivity mirrors psychophysically-measured sensitivity. Results for all conditions (including intermediate values of IAC) are reported in Chait et al (2005). Here we concentrate on transitions between extreme values of IAC (1 and 0), denoted as $1\rightarrow0$ and $0\rightarrow1$. The auditory evoked responses to $1\rightarrow0$ and $0\rightarrow1$ transitions are shown in Figure 2A, B. The origin of the time scale coincides with the onset of the signals and the change is introduced at 800ms post onset. While the onset responses for correlated and uncorrelated noise are similar in temporal dynamics (two peaks at about 50 and 150 ms post onset) and spatial distribution, the responses to the IAC transitions (shaded) are markedly different. The change in the $1\rightarrow0$ condition (Fig 2A) is characterized by two peaks at ~70ms and ~150ms post change. In contrast, the opposite, $0\rightarrow1$ transition, evoked only one peak at about 130ms. Remarkably, the dipolar distribution of the peak in the $0\rightarrow1$ stimulus is of opposite polarity to the two peaks in the $1\rightarrow0$ condition, indicating that this response cannot be a delayed activation of the neural substrates responsible for the first peak in the $1\rightarrow0$ condition, and is most probably generated by a different neural mechanism.
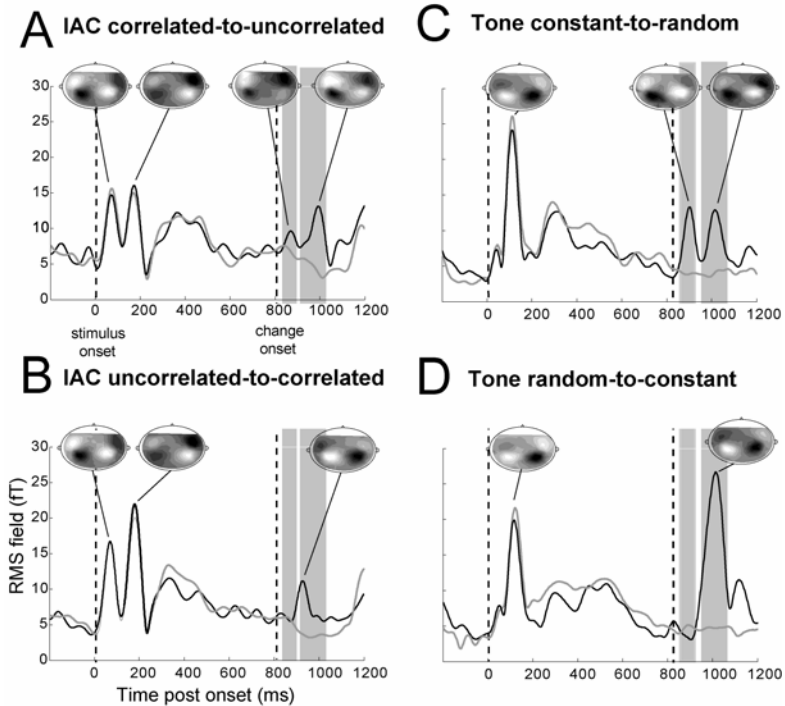
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Figure 2: Measured data. RMS magnetic field measured in the IAC experiment (left) and tone experiment (right). Plotted in black is the root mean square (RMS) magnetic field over all 157 channels derived from the grand-average (average over subjects and stimulus repetitions) of the evoked auditory cortical field. The upper plot in each column corresponds to the order-to-disorder transition (correlated to uncorrelated, or constant to random). The bottom plots correspond to the opposite transition. The appropriate control conditions (no change) are plotted in grey. The onset of the stimulus and onset of change are marked with dashed lines. Contour plots indicate the topography of the magnetic field at critical time periods. Source = white, Sink = black.

Onset response patterns differed between experiments. In the IAC experiment (left), stimulus onset responses to correlated (A) and uncorrelated (B) noise stimuli were comparable, and characterized by two peaks at approximately 70 ms and 170 ms post onset with similar magnetic field distributions (analogous to the classic M50 and M150 onset responses),. In the tone experiment (right), onset responses were characterized by a single peak at approximately 110 ms post onset, with a topography characteristic of the classic M100 response. In contrast to the onset responses, transition responses were remarkably similar between experiments (compare A and C, B and D). Both experiments revealed the same asymmetry. Transitions from order to disorder (A and C) were characterized by peaks at ~70 ms and ~150 ms post change onset whereas transitions from disorder to order (B, D) were characterized by a single peak at around 150ms. Furthermore, whereas both peaks in A and C exhibited an M50-like topography, the single peak in B and D was characterized by an opposite (M100 like) dipolar distribution.

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4 Tone experiment results

The auditory evoked responses to constant-to-random and random-to-constant 30ms pip-size stimuli are shown in Figure 2 C,D (Results for other conditions and regarding cortical adjustment to pip-size are reported elsewhere; Chait et al, in preparation). The change is introduced at 840ms post onset. The MEG activity evoked by the stimuli exhibits an onset response, about 100ms after the onset of the stimuli and a later response related to processing the change, which begins at about 900ms post onset (60ms post change). Unlike the onset responses which are very similar across conditions, transition responses are distinctly disparate in their temporal dynamics and field distributions. The change from a constant tone to a random sequence of tone pips evokes two consecutive deflections, at about 70 and 150 ms post change onset. The opposite transition evokes only one peak, occurring about 150ms post change onset. As in the IAC data, the dipolar distribution of the transition response peak in Figure 2D is of *opposite polarity* from the transition response peaks in Figure 2C indicating that activity results from a different neural substrate. Thus the response to the 'random-to-constant' transition does not merely reflect delayed activation compared to the 'constant-to-random' transition. Rather, the data suggest that the sequence of cortical activation is distinct in each case: processing of transitions in each direction involves different neural computations.

5 Discussion

'Binaural sluggishness' refers to the apparent insensitivity of the binaural system to rapidly varying interaural configuration. For example, it has been demonstrated that listeners become less sensitive to time-varying changes in interaural correlation as the change rate is increased (Grantham 1982). This 'sluggishness' is assumed to reflect the existence of a 'binaural integration window' that operates subsequent to the site of binaural interaction, i.e. at or above the IC. However, Joris et al. (2006) found no evidence of sluggishness in responses of IC cells to stimuli with dynamic interaural correlation. It is thus possible that the mechanisms we observe reflect the operation of this integration process. However, the similarity between the tone and IAC data presented here point to the fact that this mechanism is not special to binaural processing. The resemblance suggests that the responses we observe reflect the operation of a general auditory cortical change-detection mechanism, which handles in a common fashion changes along very different stimulus dimensions and specifically transitions between irregularity and regularity. Therefore 'Binaural sluggishness' might not be a result of special *binaural* integration windows but may in fact result from the same integration mechanisms that process monaural data. The apparently larger integration for binaural than monaural stimuli (e.g. Kollmeier and Gilkey 1991) may stem from differences in the statistics of the two kinds of signals. By searching for a monaural stimulus (for example by adjusting the pip size/distribution properties of our tone

stimuli) that results in the same response properties (peak latencies) as the binaural stimuli in the IAC experiment, we may be able to learn more about how binaural information is centrally represented.

Change detection in humans is usually investigated with the MMN paradigm (Polich, 2003), which is based on comparing brain responses to deviant (low probability) signals presented among standard (high probability) signals. The MMN response (derived by subtraction between the responses to standard and deviants) peaks between 100-200ms and is interpreted as reflecting a process that registers a change in a sound feature and updates the ongoing representation (Winkler, Karmos and Naatanen 1996). MMN experiments are typically conducted with silent intervals between relevant stimuli, so that the time at which a stimulus is compared to the preceding one is defined by the experimenter. The experiments here target a stage that directly precedes the one probed with standard MMN techniques: In natural environments changes are superimposed on the continuous waveform that enters the ear and a listener thus needs a mechanism to decide *at which point* in a continuous sound the change is introduced.

In transitions such as correlated-to-uncorrelated or constant-to-random (Fig1 A) the change can be detected immediately by the system - the first waveform sample that violates the regularity rule suffices to signal the transition. However in the opposite transition - from uncorrelated to correlated or from random-to-constant (Fig1 B) the system must wait long enough to distinguish the transition from a momentary 'lull' in the fluctuation, such as might occur by chance. The amount of time an optimal listener would have to wait in order to detect the change depends on the statistical properties of the stimulus. This may explain the finding that the two kinds of transitions are handled by different cortical systems: The first deflection at ~70 ms post change, with M50 like dipolar distribution that occurs in situation when the change is immediately detectable (Fig 2 A, C) may be reflecting the operation of an 'obligatory cortical integration window'. The response at around 100-150 ms with the M100 like dipolar distribution may reflect the operation of another, 'adjustable window', provided by a separate neural substrate, which integrates incoming information to reach a sufficient level of certainty that a change has occurred.

Interestingly, these transition responses are similar to the properties of the 'pitch onset response' (POR; Krumbholz, Patterson, Seither-Preisler, Lammertmann and Lütkenhöner 2003; Gutschalk, Patterson, Scherg, Uppenkamp, and Rupp 2004; Ritter, Gunter Dosch, Specht and Rupp 2005; Chait, Poeppel and Simon 2006). The POR, hypothesized to reflect cortical pitch processing mechanisms, is evoked by transitions between irregular click trains, which do not have a pitch and regular click trains which are perceived to have a sustained temporal pitch (Gutschalk et al., 2004) or by transitions between white noise and iterated rippled noise (Krumbholz et al., 2003). However, it is also possible to describe the shift as a transition between states that differ along a more abstract dimension, such as degree of 'regularity' or 'order'. Our stimuli, whether constant/random tones or correlated /uncorrelated noise, are very simple examples of 'order' and 'disorder'. We have recently replicated this pattern of results with

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regularly alternating pip sequences (rather than a constant tone) and speculate that more complex stimuli involving transitions between regularity and irregularity should evoked similar response patterns to the ones observed here.

Future experiments are needed to test the generality of the present findings, to clarify the relation between behavioral and brain responses to change and to better understand the rules that determine factors such as integration time. In addition to studying the dynamics of change detection, the paradigm introduced here may serve as a methodological tool to explore the perceptual relevance of various sound dimensions: Are changes in different features, which are relevant to auditory objects (e.g. loudness, ITD, ILD, pitch) processed in the same way and equally quickly? Such an investigation may shed light on their relative importance in determining the emergence of auditory objects.

6 Acknowledgments

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