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Research paper

Temporal envelope processing in the human auditory cortex: Response and interconnections of auditory cortical areas

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Abstract

Temporal envelope processing in the human auditory cortex has an important role in language analysis. In this paper, depth recordings of local field potentials in response to amplitude modulated white noises were used to design maps of activation in primary, secondary and associative auditory areas and to study the propagation of the cortical activity between them. The comparison of activations between auditory areas was based on a signal-to-noise ratio associated with the response to amplitude modulation (AM). The functional connectivity between cortical areas was quantified by the directed coherence (DCOH) applied to auditory evoked potentials. This study shows the following reproducible results on twenty subjects: (1) the primary auditory cortex (PAC), the secondary cortices (secondary auditory cortex (SAC) and planum temporale (PT)), the insular gyrus, the Brodmann area (BA) 22 and the posterior part of T1 gyrus (T1Post) respond to AM in both hemispheres. (2) A stronger response to AM was observed in SAC and T1Post of the left hemisphere independent of the modulation frequency (MF), and in the left BA22 for MFs 8 and 16 Hz, compared to those in the right. (3) The activation and propagation features emphasized at least four different types of temporal processing. (4) A sequential activation of PAC, SAC and BA22 areas was clearly visible at all MFs, while other auditory areas may be more involved in parallel processing upon a stream originating from primary auditory area, which thus acts as a distribution hub. These results suggest that different psychological information is carried by the temporal envelope of sounds relative to the rate of amplitude modulation.

Keywords: Amplitude modulation; Temporal envelope; Auditory cortex; Human; Hearing; Directed coherence

Abbreviations: AEP, auditory evoked potential; ALA, anterior lateral area; AM, amplitude modulation; AR, autoregressive; ARX, multivariate autoregressive; BA, Brodmann area; BMF, best modulation frequency; DCOH, directed coherence; DTF, directed transfer function; EEG, electroencephalography; FFT, fast fourier transform; fMRI, functional magnetic resonance imaging; HG, Heschl gyrus; Hz, Hertz; LFP, local field potential; MEG, magnetoencephalography; MF, modulation frequency; PAC, primary auditory cortex; PDC, partial directed coherence; PSD, power spectral density; PT, planum temporale; SAC, secondary auditory cortex; SEEG, stereo-electroencephalography; SNR, signal-to-noise ratio; T1Post, T1 Gyrus; TMTF, temporal modulation transfer function

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1. Introduction

The perception of speech involves several areas of the human cortex, most of them concentrated in the temporal lobe. However, due to the complex nature of speech, the underlying mechanisms of its perception are not yet clear. A way to address some of these mechanisms is to isolate the temporal components of vocalizations associated with speech. The classification of these components has now been clearly established: the fastest ones, above 100 Hz, code for a fundamental frequency called pitch (Smith et al., 2002), and the harmonics thereof define fine features like timbre or loudness. Temporal variations from $\sim$20 Hz up to 100 Hz determine sound periodicity (Rosen, 1992) also called periodicity pitch (Flanagan and Guttman, 1960). They are associated with virtual pitch height (Burns and Viemeister, 1976; Miller and Taylor, 1948; Ritsma, 1962) and roughness (Pressnitzer and McAdams, 1999; Terhardt, 1974). The temporal envelope of speech usually features among the slowest amplitude modulations (AM) between 2 and about 50 Hz. They convey the sensations of tempos and rhythms (Drake and Botte, 1993; Fraisse, 1967; Friberg and Sundberg, 1995) and those which are most pronounced are associated with the syllabic cadency around 3–4 Hz (Houtgast and Steeneken, 1985; Steeneken and Houtgast, 1980). Thus, the temporal envelope is crucial for intelligibility of speech.

This paper deals with the temporal envelope processing in the human auditory areas of the temporal lobe. The representation of temporal sound envelopes in the human auditory cortex has been extensively studied by means of sinusoidal-amplitude-modulated (AM) white noise stimuli. Such stimuli have wideband long-term power spectra and so they excite all auditory nerve fibers. In response to these stimuli, electroencephalographic analysis revealed oscillating electrical activity in the auditory brain areas (Pantev et al., 1988; Picton et al., 1987). This activity is phase-locked with temporal amplitude variations and is observed when a sufficient number of neurons (around 10^5 to 10^7) are activated synchronously (Eggermont and Ponton, 2002; Hämäläinen et al., 1993; Nunez, 1981). Consequently, this oscillation almost perfectly reproduces the AM frequency but its amplitude varies with the recording location. Intracerebral recordings (stereo-electroencephalography, SEEG (Bancaud et al., 1965; Talairach et al., 1974)) have revealed a visible response to temporal envelope in the following auditory areas (Liégeois-Chauvel et al., 2004):

- Primary auditory cortex (PAC)
- Secondary auditory cortex (SAC)
- Posterior part of the Superior Temporal gyrus (T1 Post)
- Anterior part of the Superior Temporal gyrus, i.e. Brodmann area 22 (BA22)
- Planum temporale (PT)
- Insula
- Sulcus between PAC and PT (Sulcus).

The status of the Sulcus is controversial. Some studies found primary-like features (Liégeois-Chauvel et al., 1994; Wallace et al., 2002) while others considered it as part of the lateral belt (Rademacher et al., 1993; Sweet et al., 2005). In addition to vestibular functions, the insular gyrus is partially involved in auditory processing (Braak, 1978; Galaburda and Sanides, 1980; Liégeois-Chauvel et al., 1991, 1994, 2004; Morosan et al., 2001). Consistent with results reported in the literature, these reports showed or confirmed:

- an encoding of amplitude modulation frequency in the human auditory cortex for modulation frequencies below 64 Hz, in agreement with a number of psychoacoustical studies,
- a predominant response of auditory cortical areas to the low modulation frequencies (4–16 Hz) known to be crucial for speech perception,
- differences in temporal resolution across human auditory cortical areas; the highest resolution is found in PAC and insula in both hemispheres,
- no (clear) reproducible spatial mapping of modulation frequency within the human auditory cortex, but existence of specific neuron groups and functional maps for AM for several patients,
- interhemispheric differences with the highest responses in left hemisphere for SAC and T1 Post areas; moreover, lower best modulation frequencies (BMFs) are reported more frequently in left T1 Post than in right T1 Post, and more frequently in right SAC than in left SAC.

A complementary approach to the study of the response strength to AM relates to the dynamics of the processing, i.e. the evoked connectivity. To our knowledge, anatomical and functional connectivity in the human auditory cortex have rarely been studied. These two types of connectivity are not necessarily correlated, at least in animals (Eggermont and Smith, 1996). Concerning anatomical connectivity, most results derive from animal experiments whose anatomical framework is then extrapolated to human beings. The auditory cortex of the primate is subdivided into three areas whose corresponding areas in the human cortex are indicated in parenthesis. The core has similar primary-like features (PAC, possibly Sulcus) and is surrounded by a belt of fields (SAC, Wallace et al., 2002, possibly Sulcus), as well as a more lateral parabelt of fields at a third level of processing (PT, Sweet et al., 2005, possibly BA22 and T1Post). One has to note that although BA22 and T1Post areas are generally considered as parabelt areas based on their localization on the lateral temporal sulcus similar to that of parabelt areas in macaque, this has still to be confirmed by comparative architectonic studies as in Sweet et al. (2005); Wallace et al. (2002). In any case, most studies have shown that auditory information may be distributed from the core areas to surrounding belts that relay information to parabelt regions (for review, Kaas and Hackett, 2000; Kaas et al., 1999). Anatomical connectivity