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Modulation of response patterns in human auditory cortex during a target detection task: An intracranial electrophysiology study

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ABSTRACT

Selective attention enhances cortical activity representing an attended sound stream in human posterolateral superior temporal gyrus (PLST). It is unclear, however, what mechanisms are associated with a target detection task that necessitates sustained attention (vigilance) to a sound stream. We compared responses elicited by target and non-target sounds, and to sounds presented in a passive-listening paradigm. Subjects were neurosurgical patients undergoing invasive monitoring for medically refractory epilepsy. Stimuli were complex tones, band-limited noise bursts and speech syllables. High gamma cortical activity (70–150 Hz) was examined in all subjects using subdural grid electrodes implanted over PLST. Additionally, responses were measured from depth electrodes implanted within Heschl's gyrus (HG) in one subject. Responses to target sounds recorded from PLST were increased when compared to responses elicited by the same sounds when they were not-targets, and when they were presented during passive listening. Increases in high gamma activity to target sounds occurred during later portions (after 250 ms) of the response. These increases were related to the task and not to detailed stimulus characteristics. In contrast, earlier activity that did not vary across conditions did represent stimulus acoustic characteristics. Effects observed on PLST were not noted in HG. No consistent effects were noted in the averaged evoked potentials in either cortical region. We conclude that task dependence modulates later activity in PLST during vigilance. Later activity may represent feedback from higher cortical areas. Study of concurrently recorded activity from frontoparietal areas is necessary to further clarify task-related modulation of activity on PLST.

1. Introduction

Attention strongly modulates neural activity in human auditory cortex (e.g., Petkov et al., 2004; Elhilali et al., 2009). Attention-related modulation can be detected using multiple non-invasive methodologies that include scalp-recorded averaged evoked potentials (AEPs), event-related neuromagnetic fields (ERFs), and functional magnetic resonance imaging (fMRI) (e.g., Näätänen, 1990; Novak et al., 1990; Ding and Simon, 2012; Alho et al., 2013). These methodologies have been especially fruitful in delineating neural mechanisms subserving selective attention by permitting the simultaneous comparison of neural activity elicited by attended and unattended sound streams. A classic example of a selective attention task utilizes a dichotic listening paradigm, wherein subjects respond to target stimuli embedded in a sequence of non-targets delivered to one ear, while ignoring simultaneously presented sounds delivered to the opposite ear. It has been shown using this paradigm or its methodological variants that both target and non-target attended stimuli elicit larger amplitude AEPs and ERFs than their non-attended counterparts (e.g., Giard et al., 2000). This enhancement of responses is noted at the earliest stages of auditory cortical processing, and extends to later stimulus-evoked AEP components such as the N100 (N1) and its analogous ERF response (e.g., Woldorff and Hillyard, 1991; Woldorff et al., 1993). In parallel to the gain enhancement of neural activity elicited by attended streams of sounds, neural activity elicited by non-attended sounds is actively suppressed (Giard et al., 2000; Chait et al., 2010).

Sustained attentional tasks (vigilance) also modulate neural activity in auditory cortex (e.g., Näätänen, 1990). Relevant to the current study, subjects may be required to detect a target sound embedded within a single acoustic stream. Here, the subject must attend to all stimuli in order to correctly identify the target. These "one-channel" tasks represent, in part, processes related to the performance necessary to detect targets within an attended sound stream during a selective attention task. Typically, the N1 component of the AEP (approximate latency 100 ms) and its ERF counterpart evoked in a target-detection task are

Abbreviations: AEP, averaged evoked potential; BPN, band-pass noise; CVC, consonant–vowel–consonant; ECoG, electrocorticogram; ERBP, event-related band power; ERF, event-related field; fMRI, functional magnetic resonance imaging; HG, Heschl's gyrus; PLST, posterolateral superior temporal gyrus.

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larger compared to responses elicited by the same sounds when subjects ignore the stimuli (Näätänen and Picton, 1987). These task-related increases are present in responses to both target and non-target stimuli. Processing-contingent potentials are also generated when subjects perform a target detection task. These potentials are termed endogenous because they are not automatically generated by acoustic attributes of sounds, but instead represent neural indices of active sound processing. Both targets and non-targets elicit processing negativities that overlap in time with later exogenous potentials (e.g., Novak et al., 1990). Targets also elicit another processing negativity termed N2 for its approximate latency of 200 ms (e.g., Gamble and Luck, 2011; Rimmele et al., 2011).

While non-invasive studies provide invaluable insights into the neural mechanisms subserving attention, they also suffer from significant limitations. AEPs and ERFs are limited in their spatial resolution. fMRI studies provide results with superior spatial resolution, but are limited in their temporal resolution and also represent an indirect measure of tissue activation. In contrast, invasive electrophysiologic studies obtained during the clinical evaluation of neurosurgical patients provide direct measures of tissue activation with both high temporal and spatial resolution. These advantages are exemplified by data acquired while subjects perform selective attention tasks. Enhanced transient and sustained AEP components are generated in core auditory cortex located on the posteromedial portion of Heschl's gyrus (HG) and in the surrounding auditory cortex on the superior temporal plane (Bidet-Caulet et al., 2007). Similar enhancements are seen in non-core auditory cortex located on the posterolateral portion of the superior temporal gyrus (PLST) (Neelon et al., 2006). In a dramatic demonstration of the neural mechanisms underlying selective attention, high gamma components of the electrocorticogram (ECoG) recorded from PLST and representing the speech of an attended talker were enhanced, while high gamma components representing the unattended speech of a second simultaneously presented talker were suppressed (Mesgarani and Chang, 2012). The latter findings are especially noteworthy because high gamma activity has been shown to be a reasonable surrogate measure of action potential firing in neuronal ensembles (e.g., Nir et al., 2007; Steinschneider et al., 2008; Mukamel et al., 2011).

It remains unclear, however, what mechanisms are engaged in PLST when subjects perform a target detection task. This region of cortex is difficult to analyze using scalp-recorded EEG because field potentials are potentially contaminated by larger-amplitude responses volume-conducted from sources located on the superior temporal plane. Further, neuromagnetic responses are less sensitive to activity located on PLST because portions of this region have a radial orientation that leads to non-optimal detection of ERFs (Hillebrand and Barnes, 2002). These limitations can be ameliorated by performing target detection tasks in neurosurgical patients implanted with high density electrodes overlying the perisylvian region.

Thus, the goal of this study was to identify task-related contributions of auditory cortical activity on PLST when subjects performed a target detection task. Both event-related band power (ERBP) in the high gamma range and lower frequency AEPs were examined. We were also able in one subject to simultaneously examine activity emanating from PLST while concurrently examining activity from depth electrodes placed within HG. This allowed comparisons of task-related effects within core auditory cortex located in posteromedial portion of HG with non-core areas located on anterolateral HG and PLST. Transformations in sound processing from HG to PLST are important steps in the progressive encoding of sound objects along the ventral auditory cortical pathway stream (e.g., Rauschecker and Scott, 2009; Chang et al., 2010). We hypothesized that attention during a target-detection task would more strongly modulate high gamma activity in PLST than at sites within HG, and that this modulation would be evident throughout the response of this non-core cortex. We further hypothesized that the AEP would contain both larger exogenous-based potentials to target and non-target sounds when compared to activity in the passive state, and that endogenous processing negativities would be identified. Instead, we found that attention most strongly modulated high gamma responses to target stimuli, and that this modulation occurred within later portions of the induced activity. Further, we found no evidence of enhanced exogenous AEPs or the generation of endogenous potentials on PLST. As predicted, attention-based modulations were more prominent on PLST than in the activity within HG.

2. Methods

2.1. Subjects

Experimental subjects were three neurosurgical patients diagnosed with medically refractory epilepsy and undergoing chronic invasive ECoG monitoring to identify potentially resectable seizure foci. The subjects were 27 (L237), 23 (R198) and 38 (L258) years old. All subjects were male, right-handed and left hemisphere language-dominant, as determined by intracarotid amytal (Wada) test results. The hemisphere of recording was left in subjects L237 and L258, and right in R198. Research protocols were approved by The University of Iowa Institutional Review Board and by the National Institutes of Health. Written informed consent was obtained from all subjects. Participation in the research protocol did not interfere with acquisition of clinically required data. The subjects could rescind consent at any time without interrupting their clinical evaluation.

The subjects underwent audiometric and neuropsychological evaluation before the study, and none was found to have hearing or cognitive deficits that should impact the findings presented in this study. All were native English speakers. Intracranial recordings revealed that the auditory cortical areas on the superior temporal gyrus were not epileptic foci in any subject.

Experiments were carried out in a dedicated electrically-shielded suite in The University of Iowa General Clinical Research Center. The room was quiet, with lights dimmed. Subjects were awake and reclining in an armchair.

2.2. Stimuli

Experimental stimuli were complex tones, band-pass noise bursts (BPN) and consonant–vowel–consonant (CVC) syllables. More simple, non-speech sounds were included as test stimuli because we were interested in identifying neural patterns associated with target detection on PLST without adding potential confounding factors related to phonetic processing, as well as determining whether these neural patterns would generalize to speech. Further, previous studies from this laboratory have demonstrated that PLST responds robustly to non-speech stimuli (e.g., Nourski et al., 2013, 2014). All stimuli were 300 ms long, had a 5 ms rise–fall time, and were presented with an inter-stimulus interval chosen randomly within a Gaussian distribution (mean interval 2 s; SD = 10 ms) to reduce stimulus predictability. Stimuli were delivered via insert earphones (ER4B, Etymotic Research, Elk Grove Village, IL) that were integrated into custom-fit earmolds. Stimulus delivery and data acquisition were controlled by a TDT RZ2 real-time processor (Tucker-Davis Technologies, Alachua, FL) with a sampling rate of 24,414 Hz.

Experimental paradigms were varied to further test the generality of effects occurring during target detection tasks. Prior to the initiation of data collection, each subject was presented with a preview of experimental stimuli to ensure that the sounds were presented at a comfortable listening level. In subject L237, stimuli were complex tones with fundamental frequencies ranging from 0.25 to 8 kHz in 1 octave steps. The stimuli were presented at 61 dB SPL. The stimuli were presented in four experimental blocks. In each block, an interleaved presentation paradigm was used, where the six tones were presented 40 times each in a random order. Blocks 1 (first) and 4 (last) did not require an overt response. The subject was told that he would hear a sequence of