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Sound identification in human auditory cortex: Differential contribution of local field potentials and high gamma power as revealed by direct intracranial recordings

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ABSTRACT

High gamma power has become the principal means of assessing auditory cortical activation in human intracranial studies, albeit at the expense of low frequency local field potentials (LFPs). It is unclear whether limiting analyses to high gamma impedes ability of clarifying auditory cortical organization. We compared the two measures obtained from posterolateral superior temporal gyrus (PLST) and evaluated their relative utility in sound categorization. Subjects were neurosurgical patients undergoing invasive monitoring for medically refractory epilepsy. Stimuli (consonant–vowel syllables varying in voicing and place of articulation and control tones) elicited robust evoked potentials and high gamma activity on PLST. LFPs had greater across-subject variability, yet yielded higher classification accuracy, relative to high gamma power. Classification was enhanced by including temporal detail of LFPs and combining LFP and high gamma. We conclude that future studies should consider utilizing both LFP and high gamma when investigating the functional organization of human auditory cortex.

1. Introduction

Intracranial recordings (electrocorticography or ECoG) have become crucial for identifying the functional organization of human auditory cortex due to their high spatial and temporal resolution (e.g. Mukamel & Fried, 2012; Nourski & Howard, 2015). ECoG is a rich time-varying measure that simultaneously reflects synaptic activity and action potentials from populations of neurons. Consequently, there is considerable interest in exactly which aspects of the ECoG signal recorded from the auditory cortex carry information relevant to sound processing. Addressing this is not only important methodologically but may also hint at fundamental ways in which populations of neurons code information.

Earlier studies using the intracranial methodology relied on analysis of time domain-averaged local field potential (LFP) signals to examine response properties of auditory cortex (e.g. Celesia & Puletti, 1969; Halgren et al., 1995; Howard et al., 2000; Lee et al., 1984; Liégeois-Chauvel, Musolino, Badier, Marquis, & Chauvel, 1994; Liégeois-Chauvel, Musolino, & Chauvel, 1991; Steinschneider, Volkov, Noh, Garell, & Howard, 1999). The averaged LFP (i.e., averaged evoked potential, AEP) emphasizes relatively low-frequency components of the ECoG signal that are both time- and phase-locked to the stimulus. This approach was in part aimed at identifying cortical generators of specific components of AEPs recorded using electroencephalographic methods and neuromagnetic fields recorded using magnetoencephalography in response to sound stimuli (e.g. Halgren et al., 1995; Howard et al., 2000; Liégeois-Chauvel et al., 1994).

With few exceptions (e.g., Chang et al., 2010; Sahin, Pinker, Cash, Schomer, & Halgren, 2009; Sinai et al., 2009; Steinschneider et al., 2011), more recent studies using intracranial methodology have focused on event-related band power (ERBP) of the high gamma frequency component (70–150 Hz) of the ECoG (e.g. Crone, Boatman, Gordon, & Hao, 2001). This approach often

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occurred at the expense of analysis of the time- and phase-locked activity as captured by the LFP. This paradigm shift has been driven by the findings that enhanced high gamma activity in the ECoG is closely related to increases in the blood oxygenation level-dependent signal as measured by functional magnetic resonance imaging methodology and to spiking activity in cortical neurons (Mukamel et al., 2005; Nir et al., 2007; Steinschneider, Fishman, & Arezzo, 2008). The focus on high gamma activity has yielded new understandings of the functional organization of human auditory and auditory-related cortex over the last decade. For instance, this analysis has helped characterize the functional representation of phonetic categories used in speech (Mesgarani, Cheung, Johnson, & Chang, 2014; Pasley et al., 2012) and the powerful effects of selective attention in modulating auditory cortical activity when listening to competing speech streams (e.g., Mesgarani & Chang, 2012). Analysis of high gamma activity has also demonstrated tiered effects of attention across auditory and auditory-related cortical areas (Nourski, Steinschneider, Oya, Kawasaki, & Howard, 2015; Steinschneider et al., 2014). All these findings parallel those obtained from patterns of spiking activity in experimental animals (e.g., Fritz, Shamma, Elhilali, & Klein, 2003; Mesgarani, David, Fritz, & Shamma, 2008; Steinschneider, Nourski, & Fishman, 2013; Tsunada, Lee, & Cohen, 2011). However, at the same time, the aforementioned advances have not compared the utility of LFPs and high gamma activity in understanding auditory processing.

This focus may be limiting because intracranially recorded LFPs have also helped characterize underlying features of functional organization of auditory and auditory-related cortex (e.g. Brugge et al., 2008; Chang et al., 2010). Furthermore, those studies that examined both high gamma and LFP revealed differences in the ways the two metrics are related to stimulus acoustics and perception (e.g., Nourski & Brugge, 2011; Nourski et al., 2009). These studies raise the possibility that both the LFP and high gamma ERBP in the ECoG reflect relevant (and non-redundant) information about sounds. If this is the case, it raises key questions about what information may be carried by the LFP that is not seen in the high gamma activity. What is needed is a direct comparison of the two measures of cortical activity to determine their relative contributions for carrying meaningful information about complex auditory stimuli as a whole.

In this study, we objectively examined this issue by using a classification approach. Subjects passively listened to consonant–vowel (CV) syllables and pure tone stimuli. The contribution of different measures of cortical activity for carrying information about these stimuli was assessed by training a classifier (support vector machine, SVM) to identify properties of the stimulus [voicing, place of articulation (POA), and tone frequency] on the basis of various permutations of the LFP and high gamma ERBP signal.

Under typical preparations, the LFP is usually a linear scaled voltage signal. It can be both positive and negative. In contrast, high gamma activity is usually a rectified power signal that is logarithmically scaled and baseline-normalized. Classification analysis can abstract across the differences between LFP and high gamma signal representation, as its dependent variable is classification accuracy (in percent correct) rather than a difference in the signal *per se*. Moreover, a non-parametric approach like an SVM may be better equipped for factoring out these differences than parametric approaches. It is important to note that the LFP signal is not orthogonal or independent of the high gamma signal, as they both are derived from the same underlying ECoG waveform. Our goal was not to try to parse out the unique information contained in each signal, but rather to use these coarse measures to ask if there is anything that cognitive neuroscience may be missing by relying on one over the other. To achieve this goal, we focused on typical preparations of these signals, characterizing the LFP as voltage time series, and high gamma activity as rectified, log-transformed and baseline-normalized ERBP.

Contrary to expectations, we found that classification accuracy based on LFPs was superior to that provided by high gamma activity. Best accuracy was often obtained when both measures were included in the analysis. Methodologically, this suggests that future studies should utilize neural activity captured both by the LFP and high frequency ERBP when investigating the functional organization of human auditory and auditory-related cortex; more broadly, it raises the possibility that by studying only local high gamma power we may be missing relevant aspects of sound encoding within the auditory cortex.

2. Methods

2.1. Subjects

Subjects consisted of 21 neurosurgical patient volunteers (16 male, 5 female, age 20–56 years old, median age 33 years old). The subjects had medically refractory epilepsy and were undergoing chronic invasive ECoG monitoring to identify potentially resectable seizure foci. 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 each subject. Participation in the research protocol did not interfere with acquisition of clinically required data. Subjects could rescind consent at any time without interrupting their clinical evaluation.

The patients were typically weaned from their antiepileptic medications during the monitoring period at the discretion of their treating neurologist. Experimental sessions were suspended for at least three hours if a seizure occurred, and the patient had to be alert and willing to participate for the research activities to resume.

In all participants, ECoG recordings were made from only a single hemisphere. All subjects but two had left-hemisphere language dominance, as determined by intracarotid amytal (Wada) test results; subject R149 had bilateral language dominance, and R139 had right language dominance. In ten subjects, the electrodes were implanted on the left side, while in eleven others recordings were from the right hemisphere (the side of implantation is indicated by the prefix of the subject code: L for left, R for right). The hemisphere of recording was language-dominant in twelve subjects (all subjects with left hemisphere implanted, R139, and R149) and non-dominant in nine other subjects (R127, R129, R136, R142, R175, R180, R186, R210 and R212). All subjects were native English speakers. Intracranial recordings revealed that the auditory cortical areas on the superior temporal gyrus were not epileptic foci in any of the subjects.

Subjects underwent audiometric and neuropsychological evaluation before the study, and none were found to have hearing or cognitive deficits that could impact the findings presented in this study. Sixteen out of twenty-one subjects had pure-tone thresholds within 25 dB hearing level (HL) between 250 Hz and 4 kHz. Subjects R127, L130 and R212 had a mild (30–35 dB HL) notch at 4 kHz, subject L258 had bilateral mild (25–30 dB HL) low frequency hearing loss at 125–250 Hz, and subject L145 had bilateral moderate (50–60 dB HL) high frequency hearing loss at 4–8 kHz. Word recognition scores, as evaluated by spondees presented via monitored live voice, were 100%, 98% and >91% in 13, 4, and 2 subjects, respectively. Speech reception thresholds were better than 20 dB HL in all tested subjects, including those with tone audiometry thresholds outside the 25 dB HL criterion. Importantly, frication and formant transition information relevant for consonant identification in the experimental stimuli (see below) was at or below 3 kHz, thus mitigating the detrimental effects on speech perception in subjects with hearing loss at 4 kHz and above.

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