ARTICLE IN PRESS

Hearing Research xxx (2018) 1–17

Contents lists available at ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

Review Article

Incorporating behavioral and sensory context into spectro-temporal models of auditory encoding

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A R T I C L E I N F O

Article history:
Received 27 July 2017
Received in revised form
18 December 2017
Accepted 26 December 2017
Available online xxx

A B S T R A C T

For several decades, auditory neuroscientists have used spectro-temporal encoding models to understand how neurons in the auditory system represent sound. Derived from early applications of systems identification tools to the auditory periphery, the spectro-temporal receptive field (STRF) and more sophisticated variants have emerged as an efficient means of characterizing representation throughout the auditory system. Most of these encoding models describe neurons as static sensory filters. However, auditory neural coding is not static. Sensory context, reflecting the acoustic environment, and behavioral context, reflecting the internal state of the listener, can both influence sound-evoked activity, particularly in central auditory areas. This review explores recent efforts to integrate context into spectro-temporal encoding models. It begins with a brief tutorial on the basics of estimating and interpreting STRFs. Then it describes three recent studies that have characterized contextual effects on STRFs, emerging over a range of timescales, from many minutes to tens of milliseconds. An important theme of this work is not simply that context influences auditory coding, but also that contextual effects span a large continuum of internal states. The added complexity of these context-dependent models introduces new experimental and theoretical challenges that must be addressed in order to be used effectively. Several new methodological advances promise to address these limitations and allow the development of more comprehensive context-dependent models in the future.

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Abbreviations: STRF, spectro-temporal receptive field; LN STRF, linear-nonlinear spectro-temporal receptive field; TORC, temporally orthogonal ripple combination; A1, primary auditory cortex; IC, inferior colliculus; MGB, medial geniculate body; STG, superior temporal gyrus; LFP, local field potential; ECoG, electrocorticography; HFB, high-frequency broadband local field potential

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https://doi.org/10.1016/j.heares.2017.12.021
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Please cite this article in press as: David, S.V., Incorporating behavioral and sensory context into spectro-temporal models of auditory encoding, Hearing Research (2018), https://doi.org/10.1016/j.heares.2017.12.021

1. Introduction

The spectro-temporal receptive field (STRF) has proven to be valuable tool for understanding how information about sound is represented and transformed as it passes through the network of auditory areas from brainstem to cortex (Aertsen and Johannesma, 1981; De Boer and Kuyper, 1968; deCharms et al., 1998; Kowalski et al., 1996). The STRF describes neural function as a filter, in that the response to any arbitrary stimulus at a point in time can be predicted as a weighted sum of the stimulus spectrogram in the immediately preceding time window. Stimuli matched to the STRF will evoke large responses, and less-well matched stimuli will produce weaker or no response. Each neuron is characterized by a different STRF, and the population of neurons constituting a brain area provides a bank of filters, each reporting the occurrence of a distinct sound feature. The model of auditory cortex as a spectro-temporal filterbank remains a dominant paradigm for central auditory representation (Chi et al., 2005; Singh and Theunissen, 2003; Yang et al., 1992). This filterbank model has inspired and continues to inspire algorithms for sound processing and signal processing more generally (Hermansky, 1998; Mesgarani and Shamma, 2005).

While sensory coding models have provided valuable insight into how the auditory system extracts useful information from sound, most models do not account for changes in internal behavioral state. Instead, they describe auditory responses exclusively as a function of the incoming stimulus. It has long been known that extensive anatomical projections from central cortical and neuromodulatory centers are situated to provide top-down control of processing in ascending auditory areas. Moreover, numerous studies have shown that changes in behavioral state (task engagement, selective attention, arousal, e.g., Fritz et al., 2003; Kuchibhotla et al., 2016; McGinley et al., 2015; Rodgers and DeWeese, 2014) and, more broadly, the behavioral context (including relatively slow changes in the acoustic environment, e.g., Dean et al., 2005; Rabinowitz et al., 2011; Ulanovsky et al., 2003) can influence sound-evoked activity. A new challenge facing the field of auditory research is to develop encoding models that integrate the influence of sensory and behavioral context. If ignored, these changes in response properties will simply appear to be noise in the auditory response. Conversely, a model that can explain these context-related effects will provide new insight into the computational strategy and neural circuitry by which top-down feedback controls auditory processing.

For the current review, the term "context" spans a wide range of timescales, falling roughly into two categories. *Sensory context* effects reflect relatively rapid adaptation to statistics of the acoustic environment, including regularities (Ulanovsky et al., 2004) and the dynamic range of noise (Dean et al., 2005; Mesgarani et al., 2014; Rabinowitz et al., 2012). *Behavioral context* effects reflect slower changes following engagement in a behavioral task (Fritz et al., 2003; Mesgarani and Chang, 2012), learning of new representations (Ohl et al., 2001; Polley et al., 2006), and, even on the developmental timescale, following peripheral hearing loss (Buran et al., 2014; Chambers et al., 2016; Noreña et al., 2003). While sensory and behavioral context clearly reflect different neurophysiological processes, ranging from automatic adaptation to the complex goal-directed behavior, they both have the net effect of changing the way neurons encode sound. Thus, for the purposes of this review, these effects can be viewed as similar modulatory processes that occur over a large continuum of timescales.

The idea of integrating contextual variables into encoding models, while appealing, introduces substantial combinatorial complexity to the problem. Measuring the response to many stimuli across many contexts drastically increases the amount of data and experimental control required to accurately estimate a complete set of model parameters. Thus, while context is important, there are practical experimental controls and model architecture designs that make studying this problem tractable.

This review begins with an overview of context effects known to influence activity in the auditory system. It then provides a tutorial on basic methods for computing the linear STRF and a brief survey of nonlinear models that build on the linear STRF. Next, it presents several studies that illustrate the full range of contextual factors that can be incorporated into encoding models. Finally, it discusses the very real technical and conceptual challenges posed by context-dependent models and new analytical and experimental approaches that promise to address these problems in the future.

A Python software library for fitting and comparing performance of context-dependent encoding models is available online: https://bitbucket.org/lbhb/nems/.

2. Sources of contextual effects in auditory processing

Exploration of context-dependent auditory encoding models has begun only relatively recently, but numerous processes are known to modulate sound-evoked activity in auditory brain areas, particularly in auditory cortex. Classically, behavioral studies emphasize discrete changes in context that reflect switching between task conditions. In contrast, studies of sensory context often emphasize graded changes in state that reflect continuous, smooth contextual variables. These distinct analytical approaches have implicated different circuit mechanisms for contextual effects. However, a comprehensive model of auditory processing should encompass both sensory and behavioral context. This section reviews findings from both lines of research, with the goal of establishing a more general framework for contextual effects on auditory encoding.

2.1. Sensory context

In studies of sensory context, a dominant idea has been that the auditory system adapts to ongoing, and presumably irrelevant, regularities in the acoustic environment in order to enhance responses to novel and potentially important sounds. This phenomenon is illustrated most simply with oddball tone stimuli. When a standard tone of fixed frequency is presented repeatedly, it is typically perceived as less salient over time. Then, when an oddball tone with a different frequency occurs at a random time in the sequence, it pops out perceptually, and neural responses are

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