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Research paper

Neural codes in the thalamocortical auditory system: From artificial stimuli to communication sounds

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ABSTRACT

Over the last 15 years, an increasing number of studies have described the responsiveness of thalamic and cortical neurons to communication sounds. Whereas initial studies have simply looked for neurons exhibiting higher firing rate to conspecific vocalizations over their modified, artificially synthesized versions, more recent studies determine the relative contribution of "rate coding" and "temporal coding" to the information transmitted by spike trains. In this article, we aim at reviewing the different strategies employed by thalamic and cortical neurons to encode information about acoustic stimuli, from artificial to natural sounds. Considering data obtained with simple stimuli, we first illustrate that different facets of temporal code, ranging from a strict correspondence between spike-timing and stimulus temporal features to more complex coding strategies, do already exist with artificial stimuli. We then review lines of evidence indicating that spike-timing provides an efficient code for discriminating communication sounds from thalamus, primary and non-primary auditory cortex up to frontal areas. As the neural code probably developed, and became specialized, over evolution to allow precise and reliable processing of sounds that are of survival value, we argue that spike-timing based coding strategies might set the foundations of our perceptive abilities.

1. Aims and scope

For all its physiological and psychological functions, from sensory processing to cognition and to motor programming, the central nervous system relies on information transmitted by neurons from one brain area to its multiple targets. This information is carried by massively parallel sequences of action potentials (AP), which continuously flow, back and forth, from sensory analyzers up to the most integrative and motor-related brain areas.

Deciphering the foundations of the neural code has been the subject of intense researches and controversies for several decades. More than 40 years ago, Perkel and Bullock (1968) set two questions in the introduction of their monograph "What do we know about coding in the nervous system? Is the code of the brain about to be broken?" Compared with the long list of potential candidates that they pointed out for consideration as neural codes, it is quite surprising that, for several decades, the average firing rate has remained the gold standard in neurosciences. This is also true in auditory neuroscience, a field where several theoretical reasons point towards the importance of the precise timing of action potentials. First, sound localization, crucial for survival, relies on the precise encoding of temporal delays between the inputs reaching the two cochlea. Second, in contrast with other sensory modalities where sensory stimuli can be static, auditory inputs are constantly changing as a function of time, and one can consider that our entire sense of hearing depends on the analysis of rapid changes in acoustic pressure at the two ears. Despites evidence pointing out the functional role of spike timing, many descriptions of neuronal functional properties (frequency tuning, temporal tuning, azimuth selectivity) have, until recently, relied on quantifications of spike rates over predefined large time windows. However, as described in this review, in the auditory modality as well as in others, temporal coding has been recently extensively studied and its involvement as neuronal basis for perception has been evaluated.

Investigating the neural code in the context of natural acoustic stimuli presents some specificities that we will briefly review in Section 2. Before examining the coding strategies involved in the representation of communication sounds (part 4), it seems

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Abbreviations: AI, primary auditory cortex; AII, secondary auditory cortex; BF, best frequency; CF, characteristic frequency; CL, caudal-lateral belt auditory cortex; CM, caudal-medial belt auditory cortex; CS, conditioned stimulus; FSL, first spike latency; HVC, high vocal center; IC, inferior colliculus; LFP, local field potential; MGB, medial geniculate body; ML, middle-lateral belt auditory cortex; STG, superior temporal gyrus; STRF, spectro-temporal receptive field; vPFC, ventrolateral prefrontal cortex.

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necessary to give a brief overview about the involvement of the temporal code in the representation of artificial time-varying stimuli such as amplitude modulation sounds (part 3). Amplitude modulation and acoustic transients are temporal features present in communication sounds (and in natural environmental sounds in general) and it has been suggested that the auditory system might become specialized to process some of these temporal features (e.g. see Nelken et al., 1999 for the processing of the coherence of low-frequency amplitude modulations across frequency bands).

2. The neural code for natural sounds in the auditory system: specific questions

It is beyond our scope to review the myriad of hypotheses that have been formulated about the neural code (see Eggermont, 1998, 2001). A review by Nelken and Chechik (2007) recently provides enlightening descriptions of different methods based on information theory to investigate the neural code in the auditory modality. Our goal here is to briefly specify the meaning of general terms used in the "neural code literature" and their specific interpretations in the auditory modality for the encoding of natural sounds. At the single cell level, one of the main debates in the neural code literature concerns the rate vs. temporal coding. In a very general sense, these two views refer to the different aspects of the spike trains from which an ideal observer could find information about the stimulus. Roughly speaking, the rate code hypothesis states that information about the stimulus is carried by the number of spikes emitted by a neuron over a predefined time-window, whereas the temporal code hypothesis generally claims that information about the stimulus is contained in the precise timing of spikes. However, and as already extensively described by Theunissen and Miller (1995) and Eggermont (1998), this denomination "rate" or "temporal" code is misleading in the auditory modality. As pointed by Theunissen and Miller (1995), the difference between rate and temporal is only a matter of the temporal scale of the analysis. In order to rigorously define a temporal code as opposed to a rate code, the authors introduced the notion of "a temporal encoding window", which length depends on the dynamic of the information to encode. In case of non-stationary stimuli, the length of the "temporal encoding window" is limited by the frequency at which the stimulus is changing. According to their proposition, in case of non-stationary stimuli, a neural code should be called "temporal" if the temporal changes in the neural response are faster than the ones imposed by the stimulus, suggesting that an internal process is "creating" a temporal code independently from the stimulus dynamics.

Our goal here is not to propose a new definition but rather to emphasize how misleading the terms "rate" and "temporal" can be in the auditory modality not only because of the time-scale of the analysis but also because of the specificity of the stimulus (artificial or natural) and the kind of analysis performed.

2.1. *Rate coding*

2.1.1. *For artificial stimuli*

If neurons are tested with simple stimuli (e.g. pure tones), one can claim that a rate code is put into play if the distributions of the total number of spikes allow a good discrimination between different stimuli (e.g. between different frequencies, cf. Fig. 1, A1). This is commonly illustrated by the frequency tuning curves, the frequency response areas and the spectro-temporal receptive fields (STRF). These representations quantify the selectivity of a cell for a particular feature of acoustic stimuli.

2.1.2. *For natural stimuli*

When tested with natural stimuli, neurons from different auditory cortical areas (from AI to belt and parabelt areas) can exhibit higher firing rate for natural stimuli such as vocalizations than other natural or artificial stimuli (Fig. 1, A2). This property can also be viewed as the signature of a rate-coding scheme and led some authors to postulate that neurons are selective for conspecific vocalizations in AI (e.g. Wang et al., 1995), for vocalizations over other complex sounds in antero-lateral belt in macaque monkeys (e.g. Tian et al., 2001) or for the animal's own vocalization in the high vocal center (HVC) of songbirds (e.g. Lewicki and Konishi, 1995; Margoliash, 1983; Mooney, 2000; Theunissen and Doupe, 1998; Del Negro et al., 2005).

2.2. *Temporal coding*

In sensory physiology, the term temporal code usually refers to the property of neurons to emit spike trains in which some spikes occur at specific time points after stimulus onset, with a high trial-by-trial reliability and at different time points for different stimuli. However, depending on the stimulus used to probe neuronal responses, a strong ambiguity remains regarding the origin of these so-formed temporal patterns: are they entirely dependent on the stimulus or do they stem from the interactions between the network connected to the recorded cells and the intrinsic properties of this cell.

2.2.1. *For artificial sounds*

Striking examples of reliable temporal patterns emerge with the use of stimuli with periodic changes of amplitude such as click trains or amplitude modulated sounds (Fig. 1, B1). In this case, spike patterns can reliably follow the amplitude modulation (AM) up to a certain modulation frequency which depends on the level within the auditory pathway. This property of some thalamic and cortical neurons to fire action potentials phase-locked to the stimulus periodicity led some authors (e.g. Wang, 2007) to propose that the neuronal response is an "isomorphic" representation of the stimulus. However, for these particular cases of synchronized responses to click trains, the simplicity of this code is quite surprising for neurons recorded so high in the auditory system. An "isomorphic" code suggests that the information is not processed but simply relayed. Alternatively, one might propose that the use of the term "neural code" is not appropriate in the sense that the neurons do not transform the stimulus into a different representation than the one already present in the stimulus itself.

2.2.2. *For natural sounds*

As in other systems (deRuyter van Steveninck et al., 1997; Hallock and Di Lorenzo, 2006), thalamic and cortical neurons of the auditory system can exhibit extremely reliable temporal patterns across several repetitions of a natural sound (Fig. 1, 2B). These patterns, being both reliable across trials and different for different stimuli led several authors to propose that a temporal coding scheme is far more probable than a rate code, or in other words, more efficient than a selectivity in terms of spike count for certain stimuli (Huetz et al., 2009; Narayan et al., 2006; Schnupp et al., 2006). However, it can be argued that these temporal patterns simply reflect the stimulus dynamics. Indeed, if one assumes that neurons are implementing a rate-coding scheme for simple spectrotemporal features of the stimulus, or in other words, act as spectrotemporal filters of the stimuli, the evoked spike timing should be reliable across trials and should differ for different stimuli (Fig. 1, B2). According to Theunissen and Miller (1995) definition, these observed temporal patterns should not be considered as a temporal code since the modulations of the firing