

## Neural coding of temporal information and its topography in the auditory cortex

A significant challenge for auditory neuroscience lies in the quest for a thorough understanding of how highly complex stimuli, such as human speech and other animal vocal signals, are encoded. Speech has components that vary on a timescale from the relatively slow (< 40 Hz), as with the rhythm of phonemes, to more rapid features (>100 Hz) that potentially provide the cues needed to identify a speaker's voice (Rosen 1992). The auditory cortex is involved in the processing of these complex sounds (Heffner and Heffner 1984; Fitch *et al.* 1997; Mesgarani *et al.* 2008; Woolley *et al.* 2009) and most cortical neuron responses are timing-locked to the lower range of modulation (Joris *et al.* 2004). Much work still needs to be done to elucidate what specific combination of neural response characteristics, connectivity and network organization are needed to permit the exquisite feature selectivity needed for speech recognition.

Two of the response characteristics of cortical neurons that have been attributed to the coding for temporal stimulus features include precise spike timing in the coding of slow repetition sounds and firing rate for faster repetition sounds (Joris *et al.* 2004; Schulze and Langner 1997; Lu *et al.* 2001). Inter-spike intervals also potentially serve as a code for temporal processing, but have not been investigated as extensively as spike timing and firing rate (Cariani 1999). A recent study published in *PLoS One*, by Imaizumi and colleagues (2010), helps to elucidate the important components of temporal processing and its cortical representation, by extensively surveying the topographic organization and information content of different aspects of such temporal processing.

The authors used slow repetition rate click trains (1–30 Hz) to investigate spike-timing precision, firing rate and inter-stimulus intervals, and obtained repetition rate transfer functions in order to quantify responses. They found that all three of these measures provide information on slow repetition rate stimuli, but the amount of inter-stimulus interval information is significantly greater than that of either of the other measures alone. They point out that, in fact, spike-timing precision and firing-rate parameters each contribute to the information content of inter-stimulus interval, and that there is additional evidence of some non-redundancy in the different representations, so that concurrent employment of these different codes potentially provides complementary information about stimuli. This may be advantageous for signal processing in natural settings where less than ideal circumstances are the norm, such as low signal-to-noise ratios and the presence of multiple sound sources.

In addition to the response characteristics of individual cortical neurons, analyses of neurophysiological data have revealed spectral response features that can be mapped topographically: e.g. tonotopic maps found across taxa (Reale and Imig 1980; Müller and Leppelsack 1985; Thomas *et al.* 2006). In contrast to the spectral features, the representation of temporal information does not show a straightforward topographic mapping in the auditory cortex.

In the paper by Imaizumi and colleagues, the spatial organization of the different response categories discussed above was also mapped in the cortex, as well as additional categories such as characteristic frequency and Q40 (a spectral bandwidth measure). They produced Voronoi–Dirichlet tessellation maps corresponding to the anterior audio field for each response category, and quantitatively analysed the spatial distribution patterns for the different temporal and spectral measures. The analyses of all cortical maps showed a general feature of local clustering for similar functional properties. Responses to the click train stimulation revealed this clustering to be non-homogenous for each of the temporal response measures. In general, cortical organization in regards to these parameters was less globally organized than what is

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observed for spectral measures. The differing spatial organization for each of the three stimulus repetition codes (spike-timing precision, firing rate and inter-stimulus interval) suggest that they operate somewhat separately, and the authors interpret the locally differing spatial patterns as evidence that helps to clarify multiple, concurrent processing streams.

Together, the data collected by Imaizumi and colleagues suggest that cortical neurons employ multiple strategies in the processing of sounds that are characterized by low repetition rates. Their paper helps to clarify the roles played by timing and place coding in the analysis of repeating stimuli. Understanding these roles is essential for increasing our knowledge of how complex stimuli such as speech are encoded. Further work along these lines, including single unit recordings and recordings from awake preparations, should provide even greater insights into the encoding of speech and other sounds.

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