Single-neuron encoding of surprise in auditory processing

The main role of structures in ascending sensory systems is to extract raw features of sensory input and compartmentalize the information-bearing elements for use by the brain. Information-bearing elements can be apparent, as in the case of stimulus frequency or intensity (Ehret and Merzenich 1988; Tramo *et al.* 2002; Yu *et al.* 2010). The features of sound that drive neuronal firing at higher auditory centers, however, remain elusive. In their exciting article, Gill and colleagues (2008) show how "surprise" is a dimension of auditory experience that alters firing patterns of central auditory neurons. By elaborating the method for calculating and extracting spectro-temporal receptive fields (STRFs), the authors demonstrate that auditory neurons, mainly those from hierarchically higher-order areas, modulate their discharge rates in response to sound elements that deviate from expected values. This work is the first to capture and separate encoding due to surprise from the ongoing encoding of spectral and temporal elements of acoustic cues (Theunissen *et al.* 2004).

The coding of auditory information was studied in a highly social songbird species, the zebra finch (*Taeniopygia guttata*), which frequently engages in vocal exchange as part of its normal behaviour (for reviews, *see* Zeigler and Marler 2004). On the receiving (sensory) end of this exchange, the acoustic elements of the incoming birdsong, including notes and syllables, are encoded by auditory neurons (for reviews, *see* Mello *et al.* 2004; Gentner 2004). As with words in human speech, for a song to be recognizable over repeated use, the order of all of its individual sound elements must also be largely preserved across time. Consequently, songbirds naturally generate expectations not only for specific songs but also for the general structural rules, internal correlations or probability statistics that apply to song elements.

To determine if surprise was predictive of altered neuronal activity, electrophysiological recordings were made in key structures of the ascending auditory pathway, including the songbird analogue of the mammalian inferior colliculus (nucleus MLd), the primary auditory forebrain area (Field L2) or an association auditory forebrain area (CLM) (Vates *et al.* 1996; Mello *et al.* 1998). One of the main goals of this work was to isolate the impact of surprise on auditory encoding for different cells (Gill *et al.* 2008). To this end, different forms of STRF were compared, including a STRF that was specifically developed to capture the impact of firing due to unmet expectations in stimulus structure (a surprise-STRF). In order to drive neuronal firing by surprise, Gill and colleagues generated song stimuli in which certain song elements were louder or softer than expected. Deviations were only introduced as changes in power for a particular element given a brief sample of "stimulus history". This manipulation allowed for the measured and elegant application of "surprise" embedded on the song elements without having to interpret surprise in the context of the entire song.

The authors show that surprise-STRF had far greater predictive strength relative to other STRF metrics and, therefore, was useful to parse out and quantify changes in firing given the probability of that change occurring based on prior experience. Surprise-STRFs were shown to have provided improvement in predictive power for select neurons at all three levels of the auditory pathway that were tested. Great gains in prediction were, however, frequently made by surprise-STRFs in the higher-order auditory area CLM, for two dominant cell types named by the authors as off-set and complex auditory neurons.

Interestingly, in neurons that are surprise-responsive, Gill and colleagues found that the degree of altered firing was relatable, in linear terms, to the magnitude of change introduced. In addition, surprise coding was directionally sensitive; surprises to augmented stimulus power could be encoded at an entirely different sub-set of neurons than cells tuned to the surprise of a lower than expected stimulus power.

They found that off-cells were particularly useful as detectors of surprise coding for a particular direction of change (certain cells coded louder than expected sounds, whereas others coded quieter than expected sounds). Complex auditory neurons were shown to be general change detectors that also encode the dimension of surprise. The surprise-STRF, therefore, provides a powerful separation of encoding surprise from that which is explainable by strength of sensory drive.

In an elegant control the authors also showed that neurons increased their firing rates to a period of unexpected silence (Gill *et al.* 2008). These findings refute the notion that silence promotes suppression of central auditory neurons or that it is the reduced amplitude of the signal that accounts for lowered firing rates. Interestingly, it was also found that unexpected transitions between song elements and modulated noise produced surprise coding, and that the encoding schemes were the same as those observed for surprise induced by violations in expected power. These outcomes suggest that surprise-STRFs are equally powerful in predicting coding strategies when unexpected transitions occur across sound categories.

The findings by Gill and colleagues are in close agreement with an earlier report that used eye tracking for viewing of natural scenes to suggest that surprise might be a detectable and quantifiable part of sensory processing (Itti and Baldi 2005). Together these sets of observations support the hypothesis that surprise is an important dimension of sensory experience and is encoded across multiple structures within the ascending sensory pathway. The extent to which surprise code relates to expected values of information may provide important inroads into how surprise shapes the emergent properties of learning and decision making, both of which feed upon information provided by sensory systems. That the nervous system encodes surprise robustly, early and as a dimension of sensation suggests that the brain may be placing heavy bets in favour of consistency, leading to a system that is strongly alerted when expectations for redundancy are not met. Locating surprise-driven encoding may have particularly important implications for the neural basis of learning or risk assessment given that surprise coding essentially earmarks sources of new information.

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