and colleagues then used this information to determine how often cells divide asymmetrically compared with symmetrically. The authors found that SHR-mediated asymmetric division occurs only during a limited window of the cell cycle.

The authors used mathematical models that revealed that bistability is not a prerequisite for SHR–SCR action. This outcome might seem inconsistent with the findings described previously[3]. However, it can also be considered as an alternative model for bistability – especially given that the authors also observed an increase in the level of SHR, and this level of SHR remained constant until division took place, then the level decreased, which is consistent with previous findings.

The authors found that the absence of SHR from a cell during a specific stage of the cell cycle affects its commitment to divide asymmetrically or symmetrically. They demonstrated this through a mathematical approach and confirmed it experimentally by synchronizing cells at particular stages of the cell cycle, using cell-cycle inhibitors. The induction of SHR expression after the cells were released from inhibition of the transition between the G1 and S stages of the cell cycle triggered a higher frequency of asymmetric cell divisions than was observed after the release from transition between the G2 and M stages of the cell cycle.

In the region of the root called the meristem, cells have the potential to undergo both types of division. Another interesting observation made by the authors was the inability of SHR to initiate asymmetric cell divisions outside the meristem, indicating that other factors, including the auxin gradient necessary for SHR–SCR action, as well as all the components of the signalling network needed for asymmetric division, are probably expressed exclusively in the meristem. Examining these components experimentally will provide more insights into the requirement for SHR in triggering divisions in a differentiated cell.

The authors worked in the laboratory of Philip Benfey, who died in 2023. When those of us who knew him think about Benfey, some of the attributes that come into our mind include vision, leadership, intelligence, generosity, kindness, optimism and courage. The plant developmental biology community has lost an outstanding scientist, a fantastic person, a great mentor and leader. His passion, dedication, innovation in research and his support for the young generation, especially female researchers, have inspired us all. His optimism and courage were contagious and gave us all hope for the future. He will always be in our hearts, and his legacy will live on.

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Neuroscience

How the brain produces and perceives speech

Yves Boubenec

A neural probe has been used to capture the activity of large populations of single neurons as people are speaking or listening, providing detailed insights into how the brain encodes specific features of speech. **See p.593 & p.603**

In the human brain, the perception and production of speech requires the tightly coordinated activity of neurons across diverse regions of the cerebral cortex. On pages 593 and 603, respectively, Leonard *et al.*[1] and Khanna *et al.*[2] report their use of a neural probe consisting of an array of microelectrodes, called Neuropixels, to measure the electrical activity of individual neurons in regions of the human cortex involved in speech processing.

Speech has a sophisticated structure that is characterized by the hierarchical organization of sounds across various timescales. Phonemes, the smallest units of speech, underpin spoken language and contribute to the differentiation of words and syllables. For instance, the three-phoneme words 'dig', 'dug', 'dog' and 'god' differ only by the alteration of a single phoneme (/dɪg/ versus /dʌg/ versus /dɒg/) or the rearrangement of phonemes (/dɒg/ versus /gɒd/).

Despite advances in scientists' understanding of the intricate neural computations involved in parsing and recognizing phonemes, it is still not clear how the brain represents the identity and sequence of phonemes at the level of single neurons. Are single neurons tuned to single phonemes (/ɪ/ versus /ʌ/ versus /ɒ/) by showing distinct responses to each? Or, instead, are neurons selective for groups of phonemes, much as neurons in the visual cortex are tuned to classes of object, such as faces[3]? And do neurons encode sequences of phonemes (such as /dɒg/ and /gɒd/)?

To address these questions, intracranial neural recordings can be made in people who are performing speech tasks[4,5]. Researchers in the same groups as Leonard *et al.* and Khanna *et al.* demonstrated in 2022 that it is possible to perform single-neuron recordings in people undergoing brain surgery while awake using Neuropixels electrodes[6,7] – a method that had previously been used only in non-human animals[8]. In their latest studies, the authors have captured the stable, simultaneous activity of tens of single cortical neurons while participants were either listening to speech[1,2] or speaking[2] (Fig. 1). Their groundbreaking work represents the first applications of Neuropixels to address meaningful research questions that can be answered only in humans.

The authors' detailed insight into the single-neuron encoding of speech perception and production yields two key findings. First, they show that single neurons are selectively tuned to groups of phonemes that are articulated in a similar way. This mirrors findings obtained with a more conventional intracranial electrophysiology method, called electrocorticography, in which electrical activity is averaged from hundreds of cells[5]. Second, these studies show how the coordinated activity of neuronal populations encodes emergent properties of speech perception and production.

Leonard and colleagues recorded neural activity from a region of the brain's auditory cortex called the superior temporal gyrus. This cortical region is specialized for high-level processing of speech sounds before the meanings of words are processed in other brain regions. Khanna and colleagues focused on a part of the brain's prefrontal cortex that is involved in word planning and sentence construction.

When participants were listening to speech, single neurons in both the auditory cortex[1] and the prefrontal cortex[2] were tuned to classes of phoneme (defined by their similar articulation) rather than specifically to single phonemes. Neurons that were spatially close to each other tended to show correlated functional

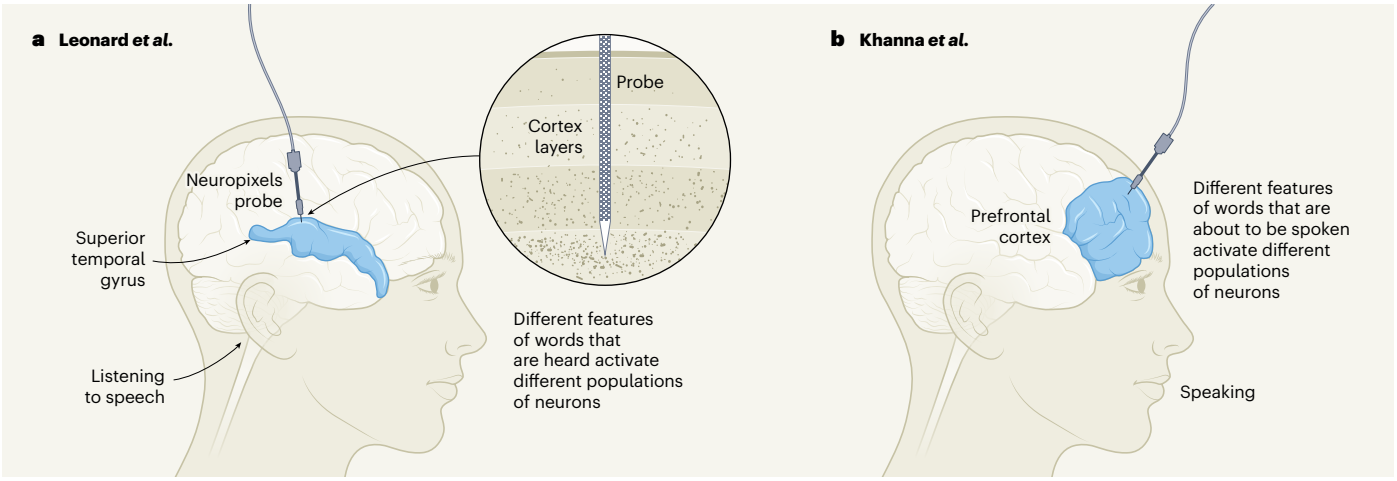

Figure 1 | Recording the activity of neurons involved in speech processing. **a**, Leonard *et al.*[1] used an intracranial probe called Neuropixels to measure the activity of single neurons in the superior temporal gyrus, a region of the brain's auditory cortex that is involved in processing speech sounds, while participants listened to speech. **b**, Khanna *et al.*[2] used the same approach to measure neuronal activity in the prefrontal cortex, a brain region that is involved in word planning, while participants were speaking or listening to speech. Both teams found that single neurons are tuned to particular features of speech, including the sounds or the positions of phonemes (the smallest units of speech) in a word. For example, the different phonemes in the word 'dog' – either heard or said – activate different populations of neurons.

properties in the auditory cortex[1]. Consequently, single neurons in the same vicinity were not good at discriminating between words composed of different phonemes but of the same phonetic group (for example, 'dog' and 'dug' with the vowels /ɒ/ and /ʌ/). By contrast, words formed by phonemes from different phonetic groups (for example, /ɒ/ and /ɪ/ in 'dog' and 'dig') activated distinct populations of neurons.

Furthermore, neurons in the auditory cortex displayed diverse responses, even to non-linguistic cues, such as the beginnings of sentences. The spatial clustering of neurons that mediate responses to similar cues is suggestive of organization into 'columns' that span several layers of the cortex. Together, these observations indicate that local populations of neurons are essential units of computation for speech processing[9] that integrate information about speech features, to which they are preferentially tuned with other sound cues. Such integration could facilitate high-level functional properties, such as the ability to recognize the same phonemes spoken by different speakers or tracking changes in the speaker's pitch.

Khanna *et al.* observed that, when participants performed a speech-production task, neurons in the prefrontal cortex were tuned to the classes of phoneme that were about to be spoken, but neurons were also sensitive to the position of phonemes in upcoming words. An analysis of changes in the coordinated patterns of activity of neuronal populations over time revealed that features of a word are coded sequentially during word planning – for example, the neuronal activity that relates to phonemes peaks before that relating to syllables. Distinct patterns of activity during listening and speech production paralleled findings from studies of the motor cortex of macaque monkeys (*Macaca mulatta*) during movement preparation and execution[10], suggesting that such patterns are a general principle of motor production.

In some cases, the two teams used different approaches to analysis. Leonard and colleagues used Neuropixels to focus on specific layers in the auditory cortex, whereas Khanna and colleagues used decoding techniques to quantify information at the level of the neuronal population in the prefrontal cortex. Integrating these complementary analyses in future studies could enrich scientists' overall understanding of the similarities and differences between the functional properties of the two cortical regions.

Both studies lay the groundwork for forthcoming investigations to determine how the internal loop between the auditory and motor centres is closed. Although the two teams focused on mapping cortical activity to auditory inputs or motor outputs, researchers still lack an understanding of the link between these processing stages. A key question arises: how does the brain's representation of the way a word sounds (an internal auditory target) translate into a sequence of coordinated neuronal activity that results in the movement of muscles required to say that word correctly? In other words, how does the auditory cortex convey auditory information to motor centres to enable accurate speech production?

Simultaneous recordings from the auditory and prefrontal cortices will help neuroscientists to understand how the production and perception of speech converge, and how information flows from the auditory cortex to the prefrontal cortex (the ascending pathway) and vice versa (the descending pathway)[11]. The ascending pathway transforms an internal auditory target into preparation for a movement in the prefrontal and motor areas. Conversely, the descending pathway informs the auditory cortex of anticipated sound inputs, such as spoken words. Notably, the neuronal projections belonging to the descending pathway – the circuit between the motor and auditory cortices – have been identified in the mouse brain[12]. Ultimately, a comprehensive understanding of how this bidirectional flow of information is coordinated during infant development will shed light on how internal representations of speech are constructed.

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