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The Neural Code That Makes Us Human Yosef Grodzinsky and Israel Nelken

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standing challenges. This research will lead to a more complete and dynamic view of energy flows within the global Earth system, where perhaps the tropical Pacific is indeed in the driver's seat.

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How does a certain pattern of vibration in the air reliably represent a meaningful speech

sound?

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NEUROSCIENCE

The Neural Code That **Makes Us Human**

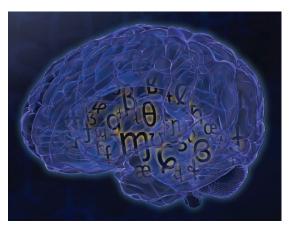
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peech provides a fascinating window into brain processes. It is understood effortlessly, and despite a huge variability, manifests both within and across speakers. It is also a stable and reliable carrier of linguistic meaning, complex and intricate as it may be. How speech is encoded and decoded has puzzled those seeking to understand how the brain extracts sense from an ambiguous, noisy environment (see the figure). On page 1006 in this issue, Mesgarani et al. (1) demonstrate the neural basis of speech perception by combining linguistic, electrophysiological, clinical, and computational approaches.

How do brains use the pattern of pressure waves in the air that is speech ("speech-assound") and extract meaning ("speech-asspeech") from it reliably, despite huge variability between speakers and background noise? Studies dating as far back as the 1950s showed that natural speech is highly redundant—speech sounds convey their identity by a large number of disparate acoustic cues (2). However, to ensure stable cue-to-speech translation by brains, an invariant code something like a dictionary of speech units seems necessary. What, then, is the nature of the representation of speech units in the brain, and how do they combine into larger, meaning-bearing pieces?

In the 1930s, linguists Roman Jakobson and Nikolai Trubetzkoy classified consonants and vowels along articulatory dimen-

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Speech perception. How highly variable speech sounds (vowels and consonants) are represented as stable phonetic units in the brain has not been clear. Acoustic-to-phonetic transformation may involve processing in the superior temporal gyrus of the human brain (1). The illustration shows phonetic symbols from the International Phonetic Alphabet superimposed on the language regions of the left cerebral hemisphere.

sions: Their description of the basic units of speech recognition referred to elements such as the place in the oral cavity where air is compressed on its way out ("labial," "dental," "velar," etc.), the manner of air release ("plosive," "sonorant," etc.), and whether the vocal cords vibrate or not ("voiced," "unvoiced") (3). For example, the sound p is a composite of features—[+labial, -voiced, +plosive] distinguishable from /b/ [+labial, +voiced, +plosive] and from /t/ [+alveolar, -voiced, +plosive]. Distinctive features, then, help to characterize the nature of invariance, while systematically grouping speech units in clusters. These features have therefore played a central role in speech recognition research.

But what actually happens in human brains during speech perception, and where? It may be that invariance is expressed in terms of articulation-related distinctive features (as proposed by linguists). Invariance may also be reflected already in sensory areas; alternatively, brain processes may achieve invariant representations of speech sounds only outside the auditory system proper. One extreme possibility is that distinctive features correlate with acoustic ones, in which case the invariant coding of sounds may already occur in sensory areas. At the other extreme, as suggested by the influential motor theory of speech perception, speech sounds may well be represented by the articulatory gestures used to produce them (4). A recent form of this view actually posits mirror neurons in the brain

onto motor actions. In that case, the invariant representation of speech would by necessity occur in motor areas, outside of the auditory system (5).

that do precisely that—map sounds

Mesgarani et al. recorded responses to speech sounds in the brains of human patients who were about to undergo brain surgery for clinical reasons. These recordings give a more detailed view of the electrical activity in the human brain than noninvasive methods such as electroencephalograms or functional magnetic resonance imaging, although they still reflect the average responses of large neuronal populations. Using these electrical signals, the authors demonstrate a high degree of invariance of speech representation as early that speech sounds of different speakers and

in a multitude of contexts nonetheless activate the same brain regions. Moreover, invariance seems to be governed by articulatory distinctive features, thereby supporting the 80-yearold theory of Jakobson and Trubetzkoy. Interestingly, features do not have equal neural representation, and those that induce strong neural invariance have strong acoustic correlates. Speech representation in the auditory cortex, in other words, is governed by acoustic features, but not by just any acoustic feature—the features that dominate speech representation are precisely those that are associated with abstract, linguistically defined distinctive features. Mesgarani et al., who base their investigation on linguistic distinctions (6), further demonstrate that features are distinguishable by the degree of the neural invariance they evoke, forming an order that is remarkably in keeping with old linguistic observations: Manner of articulation (manifesting early in developing children) produces a neural invariance that is more prominent than that related to place of articulation (manifesting late in children). A hierarchy noted in 1941 for language acquisition is now resurfacing as part of the neural sensitivity to speech sounds (7).

But linguistic communication is based on larger pieces than the basic building blocks of speech. It also requires rules that create complex combinations from basic units. Linguistic combinatorics is therefore an essential part of verbal communication, allowing it to be flexible and efficient. Here, too, Mesgarani et al. offer some clues. They show that sequencing processes, particularly those that determine voice onset time, tend to be more distributed in neural tissue than the rather localized distinctive features (8, 9). This suggests that combinatorial rules that concatenate basic elements into bigger units might depend on larger, perhaps somewhat more widely distributed, neural chunks, than the stored representations of basic building blocks. How distributed (and speech-specific) such processes are is not revealed by the Mesgarani et al. study, but evidence about the neural specificity of language combinatorics at other levels of analysis does exist: Operations involved in building complex expressions—sentences with rich syntax and semantics—are relatively localized in parts of the left cerebral hemisphere (and distinct from other combinatorial processes such as arithmetic), even if the neural chunks that support them may be as large as several cubic centimeters (10, 11).

Although the study of Mesgarani *et al.* was carried out in English, the findings have universal implications. Cross-linguistic evidence for universal neural representation of

higher aspects of linguistic communication also exists, at least to some extent (12, 13). These results may suggest a shift in view on brain-language relations: from earlier modality-based models (14), we moved to attempts to identify the neural code for specific linguistic units and concatenating operations. This move carries the hope that someday, the complete neural code for language will be identified, thereby making good on the promise that linguistics be "part of psychology, ultimately biology" (15).

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ANTHROPOLOGY

Out of Beringia?

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A shrub tundra refugium on the Bering land bridge may have played a pivotal role in the peopling of the Americas.

ased on the distribution of tundra plants around the Bering Strait region, Eric Hultén proposed in the 1930s that the now-submerged plain between Chukotka and Alaska-the Bering land bridgebecame a refugium for shrub tundra vegetation during cold periods (1), which include the last glacial maximum (LGM) between ~28,000 and 18,000 cal BP (calibrated radiocarbon years before the present). Adjoining areas to the west and east supported drier plant communities with a higher percentage of grasses during glacial periods. According to Hultén, when warmer and wetter conditions returned to these areas, the land bridge, which he named Beringia, became a center of dispersal for tundra plants. Now it appears that it also may have been a glacial refugium and postglacial center of dispersal for the people who first settled the Americas.

Since 1960, much evidence has accumulated to support the shrub tundra refugium thesis, including data collected from the former surface of the Bering land bridge. Pollen,

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plant macrofossils, and insect remains from dated sediments extracted from the floor of the Bering Sea indicate a mesic tundra habitat during the LGM (2, 3). Although pollen data from islands in the Bering Sea suggest more steppic vegetation (or "steppe-tundra"), these islands represent former upland areas on the now-submerged land bridge (see the figure). Several tree species, including spruce, birch, and alder, also probably survived locally during the LGM (3, 4). Fossil insect remains from both sides of the Bering Strait suggest surprisingly mild temperatures during the coldest phases of the LGM, despite the high latitude. All of these data presumably reflect the impact of the North Pacific circulation, which brought comparatively moist and warm air to southern Beringia during the LGM (4). In fact, the latest study of Beringian vegetation indicates that grasses were less dominant in areas outside the land bridge than previously thought (5).

The shrub tundra refugium in Beringia may also have played a pivotal role in the peopling of the Americas. Genetic evidence suggests that most Native Americans are descended from a population that was isolated somewhere between northeast Asia and Alaska during the LGM (6). According to the Beringian standstill hypothesis, this popula-