NEUROSCIENCE

# The Speaking Brain

Recordings of electrical activity in the human brain reveal the fine-tuned, stepwise neuronal processing of language and speech.

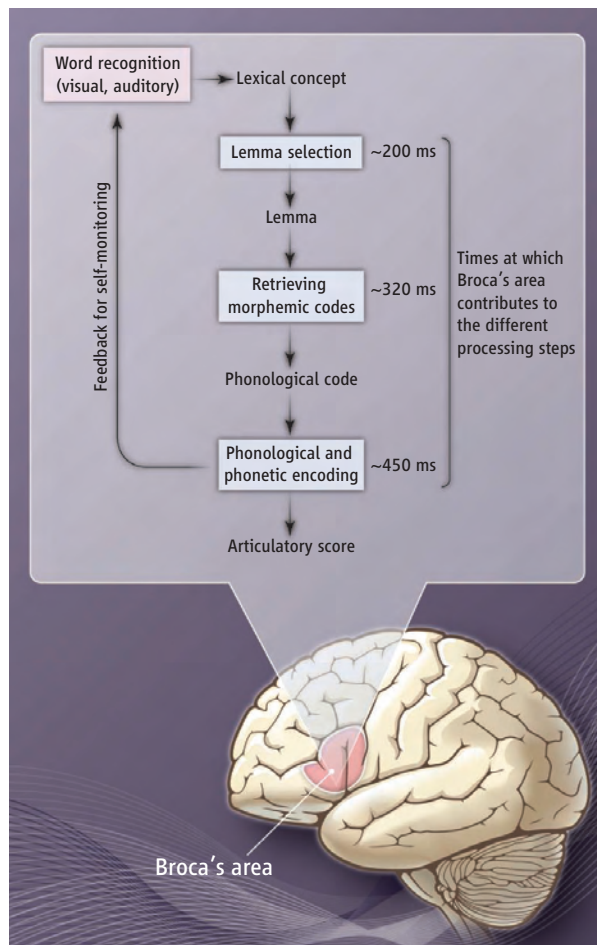**Peter Hagoort[1,2] and Willem J. M. Levelt[1]**

How does intention to speak become the action of speaking? It involves the generation of a preverbal message that is tailored to the requirements of a particular language, and through a series of steps, the message is transformed into a linear sequence of speech sounds (*1*, *2*). These steps include retrieving different kinds of information from memory (semantic, syntactic, and phonological), and combining them into larger structures, a process called unification. Despite general agreement about the steps that connect intention to articulation, there is no consensus about their temporal profile or the role of feedback from later steps (*3*, *4*). In addition, since the discovery by the French physician Pierre Paul Broca (in 1865) of the role of the left inferior frontal cortex in speaking, relatively little progress has been made in understanding the neural infrastructure that supports speech production (*5*). One reason is that the characteristics of natural language are uniquely human, and thus the neurobiology of language lacks an adequate animal model. But on page 445 of this issue, Sahin *et al*. (*6*) demonstrate, by recording neuronal activity in the human brain, that different kinds of linguistic information are indeed sequentially processed within Broca's area.

Sahin *et al*. had the unique opportunity to record from three patients with epilepsy during presurgical preparation. Depth electrodes were implanted in Broca's area and the anterior temporal cortex, and local field potentials were recorded while the patients were engaged in a language production task. The subjects were asked either to read silently words presented on a screen, or to silently produce the inflected form of the presented



**From intention to articulation.** Shown is an adapted version of the lexical encoding model for speech production (*2*), specifying steps in the paradigm used by Sahin *et al*. Based on the visual input, a lemma is selected that specifies the syntactic features of a lexical concept. For instance, for the lemma *horse*, it specifies that it is a count noun. In addition, the morphemic codes are retrieved. For instance, when the speaker wants to produce the plural form of *horse*, the codes for both the stem and the plural suffix are retrieved. Next, the phonological codes for each morpheme are retrieved, combined, and transformed into a motor command to the articulatory system. The approximate times (in milliseconds) at which Broca's area contributes to the different processing steps are shown. The late (i.e., at 500 to 600 ms) monophasic component observed in the temporal lobe (*6*) might reflect self-monitoring of the speech output.

nouns and verbs in accordance with the syntactic requirements imposed by a short sentence fragment (e.g., Yesterday they… walked). This latter process has two components (see the figure). One is to determine the correct tense of the target word and to generate (for regular inflections) or retrieve (for irregular inflections) the correct morphological form. The other is the generation of the concomitant phonological code and preparation for articulation.

Particularly in Broca's area, more specifically Brodmann area 45, a clear triphasic local field potential response was observed. At about 200 ms after presentation of the word, word identification had taken place, with a stronger response for low-frequency words than for high-frequency words. Morphological composition and retrieval for nouns and verbs happened at around 320 ms. Finally, at about 450 ms, phonological encoding had been completed. All these operations

were not only temporally separated, but also spatially segregated at a scale of only a few millimeters, which is below the effective spatial resolution of standard functional magnetic resonance imaging of brain activity.

These data are relevant for both cognitive models of speech production and for accounts on the role of Broca's area. The time course is clear evidence for the sequentiality of different access and unification operations in speaking, and is consistent with the few estimates in the literature (*7*, *8*). Moreover, both the anatomical and the temporal segregation of word-encoding operations in Broca's area are in line with the view that this region is involved with each of these encoding operations and their unification over time. Feedback operations among these processes cannot be excluded. However, the fine-grained temporal and spatial separation of these steps suggests that we are witnessing the "first go" process at work here.

Both functional magnetic resonance imaging and lesion studies have shown that Broca's area is also involved in processing inflectional morphology during comprehension (*9*). In combination with the findings of Sahin *et al*., this suggests that Broca's area is recruited during both language production and comprehension. Whether these recruitments can be separated at the scale of the microcircuitry within Broca's area remains to be seen.

Broca's area has been proposed to have a more specialized role in language processing—facilitating linguistically motivated operations of syntactic movement (*10*) and processing hierarchical structures (*11*). The

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results of Sahin *et al.* indicate that the role of Broca's area is not so limited, but should be characterized in more general terms. It is likely involved in unification operations at the word and sentence level, in connection with temporal regions that are crucial for memory retrieval (*12*).

As is known for neurons in the visual cortex (*13*), the specific contribution of Broca's area may well vary with time, as a consequence of the different dynamic cortical networks in which it is embedded at different time slices. This fits well with the finding that Broca's area is not language specific, but is also recruited in the service of other cognitive domains, such as music (*14*) and action (*15*), and with the finding that its contribution to language processing crosses the boundaries of semantics, syntax, and phonology.

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PALEONTOLOGY

# Becoming *T. rex*

James Clark

A small tyrannosaur from the Early Cretaceous sheds light on the origin of predatory features of *Tyrannosaurus rex*.

Gigantic, ferocious, long-dead animals like *Tyrannosaurus rex* never fail to capture people's attention, and the discovery of a new tyrannosaur—giant or otherwise—is always big news. On page 418 of this issue, Sereno *et al.* (*1*) report on a spectacular skeleton of a new genus and species near the ancestry of the group including *T. rex* and its closest relatives, the Tyrannosauridae. At an estimated 3 m total length, *Raptorex kriegsteini* is much smaller than the largest *T. rex* [12.8 m long (*2*)] and other tyrannosaurids, but has several key features previously known only in this family. *Raptorex* thus provides a glimpse at how tyrannosaurids evolved.

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Fossils preserved in the rock with *Raptorex* point strongly to its origin from the beds at the bottom of the Jehol Group in northeastern China, although the locality remains unknown. The Jehol Group fossil beds (*3*) are famous for preserving dinosaurs with feathers in their thin-bedded shales, including the basal tyrannosaur *Dilong* (*4*), but the skeletons are usually crushed into two dimensions, and structures such as the skull are difficult to study. Fortunately, a series of beds in the lowest part of the Jehol Group yields exquisitely preserved, uncrushed skeletons, albeit without any soft tissues.

The *Raptorex* specimen was purchased a few years ago by Henry J. Kriegstein at the Tucson Gem and Mineral Show (*5*), a venue notorious for the sale of illegally collected fossils, such as the famous *Archaeoraptor* chimera from the Jehol Group (*6*). Kriegstein approached Sereno

with the fossil, and Sereno agreed to describe it on the condition that it would be deposited in a collection in China (*5*). Although the fossil is currently with Sereno in Chicago, the specimen will be deposited in the Long Hao Institute of Geology and Paleontology in Hohhot, Inner Mongolia. Lin Tan of that institute is a coauthor of the paper, along with Kriegstein.

What to do with "hot" specimens is a conundrum for scientists. Such specimens almost always lack reliable locality data and therefore information about the sediments in which they were preserved. Stolen fossils can preserve data about the anatomy of a new or poorly known species, but enriching thieves or their fences is no more ethical for a fossil than for a car or a Grecian statue. The naming of a new ankylosaur, *Minotaurasaurus ramachandrani* (*7*), was strongly criticized (*8*), because the fossil was almost certainly

**Small beginnings.** The new tyrannosaur *Raptorex kriegsteini* (**bottom left**) (*1*) is dwarfed by the skeleton of *Tyrannosaurus rex*.

CREDITS: RAPTOREX SKELETON MODIFIED FROM (*1*); *T. REX* SKELETON BY G. S. PAUL