tion, can be inhibited by the presentation of other directions of motion. Using CRT displays of moving dots very much like our own, Movshon (*19*) has demonstrated such inhibition in the visual cortex of cats.

If only one direction of motion were present in the field, inhibition within the array would attenuate the responses of mechanisms tuned to other, similar directions. This attenuation would sharpen the distribution of responses within the array, rendering the directional information present in that distribution more unequivocal (*20*). If two directions of motion were present, as in our experiments, inhibition would distort perception of direction, exaggerating the differences between the two (*21*).

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5. The two set of dots were actually presented in rapid alternation, at a 42-Hz frame rate. This alternation was fast enough that all dots appeared to be simultaneously present. The dots appeared as two distinct streams. Each set of dots contained a wide range of spatial frequencies but no oriented contours, making it possible to vary direction of motion without the intrusion of covariation in orientation.
6. When only a single pattern was displayed on the screen, its direction was perceived with great accuracy (standard error, 0.53°). Although our subjects did not usually judge this, the pattern moving horizontally was also repelled.
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# Human Language Cortex: Localization of Memory, Syntax, and Sequential Motor–Phoneme Identification Systems

Abstract. *Subdivisions of the human peri-Sylvian language cortex were derived from stimulation mapping during craniotomies under local anesthesia. Naming, reading, short-term verbal memory, single and sequential orofacial movements, and phoneme identification were tested. Sequential orofacial movements and phoneme identification were altered from the same brain sites and thus identified a common system for language production and understanding. This system surrounded a final motor pathway for speech and was surrounded by a separate short-term verbal-memory system. Between the sequential motor-phoneme identification and memory systems were sites where only naming or reading were altered, including sites related exclusively to syntax.*

Human language is usually localized in the peri-Sylvian cortex of the dominant hemisphere, with an inferior frontal subdivision for the production of speech and a parietal-temporal subdivision for the understanding of language (*1*). Recent studies, however, suggest that the distinction into disorders of language production or understanding is rarely if ever absolute (*2*). Rather, both expressive and receptive deficits are present in all aphasic patients, though one or the other may predominate. In addition, aphasic patients of all types often show disorders in sequential control of movement and short-term verbal memory, which suggests other subdivision of the language cortex (*3*). We have identified some of these subdivisions by the location of changes in naming, reading, short-term verbal memory, single and sequential orofacial motor movements, and phoneme identification with stimulation mapping during craniotomies of the dominant hemisphere under local anesthesia in patients with medically intractable epilepsy.

This study is based on four adult patients (mean age 21.5 years, range 17 to 32) undergoing left anterior temporal lobectomy (*4*). Before the operation, intracarotid amobarbital testing revealed that all patients were left-brain dominant for language (*5*). During craniotomy, before any brain resection, the effects of bipolar electrical stimulation on tests of naming, reading, and short-term verbal memory were observed at 10 to 15 sites in the peri-Sylvian cortex of each patient. At half of these sites, stimulation effects on tests of orofacial movement and phoneme identification were also measured (*6*). The cortex was mapped with 4- to 8-second trains of 60-Hz, $2^1/_2$-msec, biphasic square-wave pulses from a constant current stimulator delivered through electrodes 5 mm apart at the largest current that did not evoke afterdischarges for the sampled cortex. Sites of stimulation were identified by a sterile number ticket, and the location was photographed and reconstructed by the relation to the cortical veins on venous phase angiograms. Figure 1 is traced from the angiogram for each patient.

The test of naming, reading, and short-term memory consisted of 25 consecutive trials. Each trial contained three achromatic slides: (i) A naming slide, shown for 4 seconds, was a picture of a common object with a phrase such as "This is a" above it. The patient read the phrase and named the object aloud. (ii) A reading slide, shown for 8 seconds, had a sentence eight to nine words long with a portion near the end omitted. The patient read the sentence aloud and generated specific syntactic forms to complete it correctly. (iii) A slide with the word "recall" on it appeared for 4 seconds. This cued the patient to say aloud the name of the object pictured on the naming slide. This represented the retrieval portion of a single-item measure of short-term verbal memory, with the object name as input and reading as distractor during which the object name must be stored. Stimulation was applied for the entire duration of one of the slides on some trials interspersed with control trials without stimulation, the sequence predetermined pseudorandomly. The same site was not stimulated consecutively, and three samples of stimulation at each site were obtained during each test condition. Responses and stimulation markers were recorded on magnetic tape.

Orofacial movements were measured by having the patient mimic postures representing terminal positions of simple movements, such as lip protrusion, pictured on a slide. One series of slides showed the same position repeated three times; the other a sequence of three different positions. Stimulation occurred during a randomly selected half of the slides of each type with three samples of stimulation at each site during each test condition, without consecutive stimulation of the same site. The patient's facial


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movements were recorded on videotape and initially analyzed for accuracy, completeness, and correct order without knowledge of which were stimulation trials. Phonemic identification was tested at the same sites as orofacial movement (*7*) by having the patients report aloud which one of six plosive consonants /p/, /b/, /t/, /d/, /k/, or /g/ they heard embedded in the nonsense syllable /a__ma/ in taped live-voice presentations. Stimulation was applied for the 2 seconds the syllable was presented and was followed by a 2-second response period without stimulation to avoid any influence of motor impairment on performance. As with orofacial movements, stimulation occurred on half of the trials, with three samples at each site. Errors are labeled in Fig. 1 only when the binomial single-sample probability of chance occurrence was .05 or less (trials without stimulation in that portion of the test served as the measure of control performance).

The pattern of errors evoked at most sites can be assigned to one of several systems. Although patients differed in the detailed location of the sites in each system, the general relationship between these systems was the same in all four patients (*8*). One system (filled arrows in Fig. 1) represents the cortical final motor pathway for speech. These five sites, at least one in the motor or premotor inferior frontal cortex of each patient, showed evoked impairment of all facial movement and, in general, an arrest of all speech, regardless of how tested. Phoneme identification was disrupted at two of the four sites tested.

A second system was identified by sites where stimulation altered sequential facial movements but where repetition of the same movement was intact (open arrows in Fig. 1). At nine of these ten sites, phoneme identification was disturbed as well. No phoneme errors were evoked from sites with intact facial movements. Thus, nonverbal orofacial movements and phoneme identification share the same portion of the language cortex. This association identifies a sequential motor-phoneme identification (SM-PI) system for language, the central mechanism suggested by the motor theory of speech perception, which this association supports (*9*). These sites are in inferior frontal, superior temporal, and parietal peri-Sylvian cortex, surrounding the final motor pathway for speech. Naming or reading are altered at eight of those sites, but memory at only two.

A third system, largely separate from the SM-PI system, is identified by 15 sites, two or more in each patient, where changes in short-term verbal memory independent of final motor pathway are evoked (broken rings in Fig. 1). At nine memory sites in the parietal or temporal, but not frontal, lobe, the memory errors follow stimulation during input or storage phases of the memory task but not during output, indicating that these sites may be involved in active memory storage and the frontal and remaining parietal sites in retrieval. Other language behavior is altered at only four of these sites (*10*). This short-term memory system surrounds the separate SM-PI system frontally, parietally, and temporally.

Sites showing only reading or naming changes cluster between the SM-PI and memory systems (*11*). Reading errors differ depending on whether there is an association with these systems. Reading errors evoked at a site that is part of either of these systems were usually jargon (six of seven, the other a grammatical error), whereas reading errors evoked at sites without such an association were most commonly grammatical errors (five of eight; others: one jargon, two arrests). One such evoked grammatical reading error was the response: "If my son will getting late today he'll see the principal," to the sentence, "If my son is late for class again he . . . principal," (*12*). These grammatical errors evoked from six sites scattered in the frontal, temporal, or parietal lobe of three patients identify cortical areas concerned with syntax. Located between the peri-Sylvian SM-PI system and the more peripheral surrounding memory system, then, are areas of the brain with specialized language functions including syntactic organization (*13*).

Brain damage that leads to persisting language deficits usually includes sites we identify as common to motor sequencing and phoneme identification. Damage to this system seems to account for the common receptive and expressive deficits of most aphasias. Relatively greater deficits in language ex-

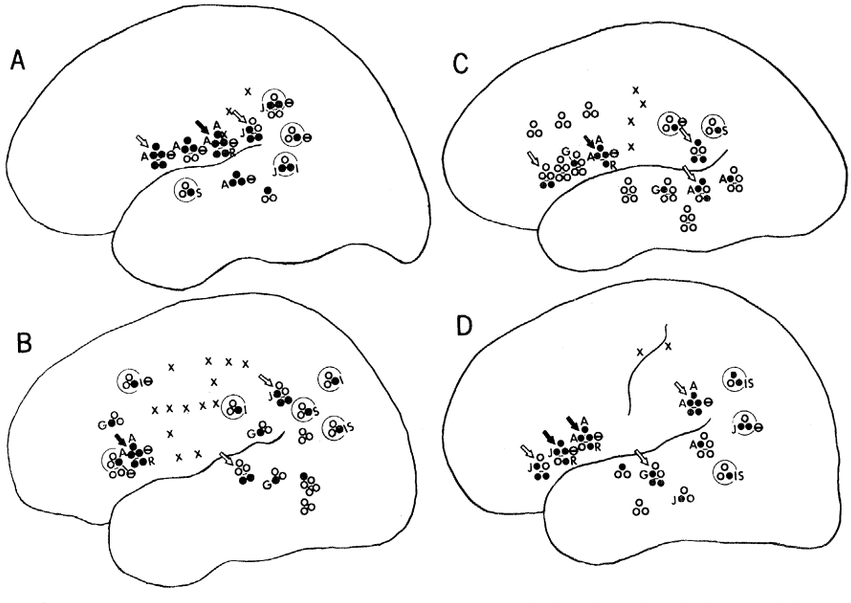


Fig. 1. Sites where stimulation alters language functions in dominant hemispheres of four patients. Naming, reading, and short-term memory measured at each site identified by a triangle of circles: naming performance, top; reading, lower left; short-term memory, lower right. Filled circles indicate statistically significant ($P < .05$) errors in that function during stimulation. Sites with two additional circles below a line also had tests of phoneme identification (left) and orofacial movements (right). The letter beside the filled circle identifies the type of error. Naming errors: *A*, arrests of speech; no letter, inability to name but demonstrated ability to speak (anomia). Reading errors: *A*, arrests, failure to read, or production of only a few words of the sentence; *J*, jargon, reading fluent, but with frequent errors in individual words including nouns; *G*, grammatical errors, production of incorrect, or deletion of syntactic elements. These last two types of reading errors were not seen on control trials. Short-term verbal memory errors: *I*, *S*, errors following stimulation during input or storage; $\theta$, errors at the time of retrieval. Orofacial movement errors: *R*, errors in repetition of the same movement; no letter, errors only on sequencing different movements. Phoneme identification errors were not further classified. Arrows and large circles are sites included in the major subdivisions of the language cortex. Filled arrow, final motor pathway for speech. Open arrow, sequential motor-phoneme identification (SM-PI) system. Large circle, memory system. X, sites of evoked motor or sensory responses identifying rolandic cortex. (A) Male, verbal intelligence quotient (VIQ) = 98, stimulation at 5 mA between peaks of biphasic pulses. (B) Female, VIQ = 90, 7 mA. (C) Female, VIQ = 98, 3 mA. (D) Male, VIQ = 93, 8 mA.

pression probably reflect an extension of damage into the cortex of the final motor pathway; relatively greater receptive deficits extend into storage portions of the short-term verbal memory system. Agrammatism may indicate damage to areas we identify with syntax. And "conduction aphasia," now recognized as largely a short-term verbal memory defect, most commonly follows lesions at the parietal-temporal junction, where we found storage aspects of the memory system (*14*). The data from our stimulation studies also suggest that phylogenetic development of language is characterized by the appearance of lateralized sequential motor and memory systems. Evidence for memory systems has been obtained in the monkey (*15*). We predict the presence of lateralized sequential motor systems in higher primates who can be taught manual communication systems.

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5. Naming, reading, short-term memory, and—in patients B and D—facial movements were measured during this intracarotid amobarbital testing. These functions changed after perfusion of the left carotid only, except for short-term memory changes after perfusion of either side in patient D.
6. Tests of orofacial movement and phoneme identification were research studies, whereas tests of naming were an integral part of the operation, performed to localize the language cortex. A limited number of sites were selected in advance for the research studies so as not to prolong the operation greatly. Procedures used for obtaining informed consent for research are reviewed annually in advance by the University of Washington Biomedical Sciences Review Committee in accordance with Public Health Service guidelines for human experimentation.
7. Phoneme identification was omitted at one site in patient C for clinical reasons.
8. Such individual variability in the exact cortical location of language functions has been quantified for naming. Only cortex immediately in front of the motor strip showed changes in evoked naming in all of the series of left-brain-dominant patients tested. Elsewhere in the classical peri-Sylvian language cortex, 20 to 70 percent of patients sampled showed no naming changes [G. Ojemann and H. Whitaker, *Brain Lang.* **6**, 239 (1978); G. Ojemann, *J. Neurosurg.* **50**, 164 (1979)].
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11. There is a high degree of functional specificity in the language cortex. Thirty-five sites outside of the final motor pathway for speech showed naming, reading, or memory changes; only four have all three and five, any two. Thus, at three-quarters of the sites, only a single language-related function was altered.
12. An example of a jargon error is the response "It is searnesy sucky," to the sentence, "If it is sunny next Saturday she . . . beach."
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16. Supported by NIH grant NS 04053 and NIH individual fellowship 1F32 NS 05847-01 (to C.M.). C. Dodrill provided the preoperative Amytal and IQ data. Patients A and D are under the care of A. Ward, Jr.

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## Sibling Matings in a Hunting Wasp: Adaptive Inbreeding?

Abstract. *Upon emergence as adults, brothers of* Euodynerus foraminatus *compete among themselves for the microterritory around their natal nest. The winning male inseminates his sisters as they emerge several days later. Unlike most species that inbreed in a similar fashion, both sexes of this common wasp are strong fliers. The possibility is raised that siblings may be preferred as mates even when outbreeding is possible.*

Among sexually reproducing animals, outcrossing is the rule. Indeed, high frequencies of close inbreeding are known for only a few forms such as gregarious parasitoid Hymenoptera, among which choice seems largely restricted to siblings (*1*). In these generally tiny insects, siblings develop in close proximity on the same host. Males are often flightless (indicating inability to join a general mating pool), reach adulthood before the females, remain in the natal area, and inseminate their sisters, which then seek out new hosts on which to oviposit. Because of the near universality of outbreeding by sexual organisms and its known benefits (*2*), biologists have tended to consider sibling mating systems as forced (in an evolutionary sense) on the species in question by low population densities and thus low chances of females finding suitable mates away from the natal area (*3*). I here report frequent brother-sister matings in an abundant, nonparasitic, solitary wasp, *Euodynerus foraminatus* (Saussure) (Vespidae), which does not seem forced to inbreed since both sexes are strong fliers and capable of dispersing widely. This case raises questions because inbreeding has important genetic consequences with regard to sex determination (*4*), sex ratios (*5*), the maintenance of sexual reproduction (*2*), and rates of evolution (*6*) and speciation (*7*); it is not obvious that costs are offset by benefits.

Normally, females of *E. foraminatus* nest in vacant insect tunnels in wood. Within the tubular hole, a female sequentially constructs and provisions a series of linearly arranged cells separated by mud partitions. Inside each cell she first lays an egg and then provides enough paralyzed caterpillars for the complete growth of the single wasp larva. When foraging, a female may fly several hundred meters to locate and sting caterpillars. Nesting wasps readily accept sticks with drilled holes (trap nests) as nest sites. Through the use of such nests, population density can be manipulated, and trap nests can be opened for study (*8*). Female wasps usually rear both sexes in the same nest hole; females in the innermost and males in the outer cells. The sexes are not intermixed (*9*). Controlled arrangement of the sexes is possible because of the haplodiploid genetic system found in the Hymenoptera. Diploid females are produced when eggs are fertilized at the time of oviposition by sperm stored in the female's spermatheca. Haploid males are produced when sperm are withheld so that unfertilized eggs are deposited. Even though females are provisioned first, males in the outer cells develop more rapidly and emerge from the nest several days ahead of their sisters. Emergence occurs in the morning, and it is usually synchronized so that all individuals of the same sex exit on the same morning within a fairly short period.

When a single nest produces two or more males, they interact aggressively; one brother drives away the others. The fights are brief, and in a matter of seconds the issue is permanently decided. The dominant male becomes resident at the nest and assumes an activity pattern that he maintains for about a week. He usually spends nights away from the nest; but each morning, as the temperature rises, he returns and awaits the emergence of his sisters. He may make periodic short flights from the nest and


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