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Broca's Region: From Action to Language

Broca's region, classically considered a motor speech-production area, is involved in action understanding and imitation. It also seems to help in sequencing of actions. Broca's region might have evolved for interindividual communication, both by gestures and speech.

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In his now classic report from 1861, Pierre Paul Broca described a man who was unable to speak although his tongue and lip movements were not impaired. The man, later called "Monsieur Tan," was able to say only "tan" and utter a swear word. He had paralysis on his right side but seemed to be intelligent and not impaired in other aspects. On autopsy, a fluid-filled cavity was found in his left frontal lobe, just anterior to the motor cortex of mouth and tongue (36). Lesions to what is nowadays called Broca's region lead to nonfluent, sparse, dysprosodic, and agrammatical speech (19). This deficit contrasts the "sensory" aphasia caused by damage to the left parietotemporal (Wernicke's) region.

In contrast to the early concept of Broca's region as an exclusive speech-production area, today's view comprises much wider language-related functions (14) as well as other communication-related functions. Recent studies have shown that Broca's

region contains representations of hand actions and orofacial gestures. In this brief review, we will focus on the motor functions of Broca's region. We start by describing the anatomy and connections of Broca's region, and then we discuss the role of this brain area in action execution, observation, and understanding and the relationship of these functions to imitation. Finally, we will speculate about why Broca's region is involved in so many apparently different functions.

Structure and Connectivity of Broca's Region

Anatomy and histology

Broca's region and its right-hemisphere homolog (FIGURE 1) include Brodmann's cytoarchitectonic areas (BA) 44 and 45; they occupy the pars opercularis and pars triangularis of the inferior frontal gyrus (IFG) in the dominant hemisphere

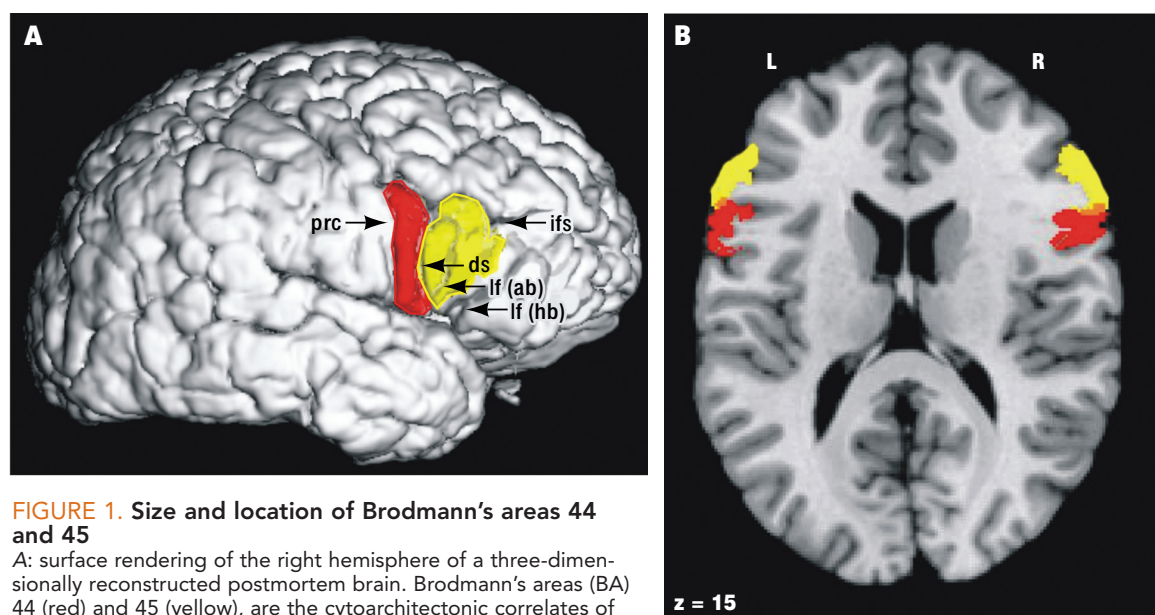


FIGURE 1. Size and location of Brodmann's areas 44 and 45

A: surface rendering of the right hemisphere of a three-dimensionally reconstructed postmortem brain. Brodmann's areas (BA) 44 (red) and 45 (yellow), are the cytoarchitectonic correlates of Broca's region and are its right-hemispheric homolog. Areas of both hemispheres were delineated in histological sections of a total of 10 brains and were superimposed on a lateral view of the right hemisphere, where the sulcal pattern is more "typical" than in the left hemisphere (2, 4). B: 50% probabilistic maps of BA 44 (red) and 45 (yellow) after warping of the 10 magnetic resonance images of the postmortem brains and their cytoarchitectonic areas to the "MNI reference brain" (http://www.fz-juelich.de/ime/ime_start, <http://www.bic.mni.mcgill.ca/>). The maps show only those voxels of the reference space that overlapped in 5 or more out of 10 brains. prc, Precentral sulcus; ifs, inferior frontal sulcus; ds, diagonal sulcus; lf, lateral fissure; ab, ascending branch of the lf; hb, horizontal branch of the lf.

(the left in 95% of the population). The widely used Brodmann map (16) represents a simplified drawing of only one typical brain, and later histological studies have indicated considerable individual variation in the size and extent of areas 44 and 45 with respect to the individual sulcal topography; for example, area 44 volume may differ across individuals even by a factor of ten (2, 4). Broca's region matures later than, for example, the primary sensorimotor cortices, as is evident from both the histological fine structure (3) and from cortical thickness maps based on magnetic resonance imaging (37).

Although areas 44 and 45 differ in their cytoarchitecture (2), they share, for example, the presence of very large pyramidal cells in deep layer III and in layer V, the lack of a clear border between layers II and III, and the low cell density in layer VI (2). However, whereas area 44 is "dysgranular" (containing a thin layer IV of small granular cells with pyramidal cells from deep layer III and upper layer V intermingled with those of layer IV), area 45 has densely packed granular cells in layer IV ("granular" area) (2, 4, 65). Although Rizzolatti and Arbib (82) consider area 44 analogous to monkey area F5, the homology between the human area 44 and the monkey F5 has not yet been demonstrated in a strict sense.

Hemispheric asymmetry

Areas 44 and 45 can be found in both hemispheres, but nearly all patients with Broca's aphasia have lesions in the left inferior frontal cortex. This clinical observation raises the question of whether and how far Broca's region and its right-hemispheric counterpart differ anatomically and functionally.

Anatomic asymmetry. The volume of the histologically defined area 44 is larger in the left than in the right hemisphere, whereas area 45 is more symmetric (2, 30). Moreover, the cytoarchitecture of both areas shows significant interhemispheric differences (5).

In great apes, the inferior frontal region corresponding to human Broca's region is larger in the left than in the right hemisphere (18), suggesting that the neuroanatomic substrates for left-hemisphere dominance in vocalization developed as early as five million years ago, long before speech emerged. It has been suggested that vocalizations were gradually incorporated into the gestural system, and in the subsequent switch from manual gesture to vocal language the left hemisphere could have taken dominance for both speech and manual action (21).

Functional asymmetry. The dominance of the left-hemispheric area 44/45 in language-related functions is well established (14). It is far less clear

whether area 44/45 is asymmetric in other communication-related functions (to be reviewed in the sections below). For example, the right IFG is activated during voluntary inhibition of imitative and overlearned responses (15) as well as during perceptual sequencing tasks (97). The right IFG is also activated when people try to make sense of ambiguous emotional expression in face images but not when they view and judge pictures of ambiguous gender (73, 78). Both left and right IFG are activated during detection of errors in musical syntax (63). Furthermore, both left and right IFG are essential for imitation (44). Finally, data on imagery of movement suggest a left-hemispheric dominance of area 44 for egocentric movements but a right-hemispheric dominance of the same area for movement characteristics in space (11). A systematic review of functional asymmetry is beyond the scope of this article. Below, findings about "Broca's region" refer to the left hemisphere, and activation of the right-hemisphere counterpart will be mentioned separately, when needed. "Area 44/45" will refer to either hemisphere.

Connections of Broca's region

The available data on brain connectivity derive mainly from tracing and electrophysiological experiments in monkeys, from which they have been extrapolated to the human brain. Some recent studies have applied diffusion tensor imaging to directly analyze connectivity in the living human brain. The major inputs and outputs of areas 44 and 45 differ to some extent, emphasizing the different functional roles of these two areas.

According to data from monkey F5, the human IFG (bilaterally) is likely to be connected to the anterior intraparietal cortex, the superior temporal sulcus (STS), the parietal cortex (area PF in monkeys), the cerebellum, and Wernicke's area (reviewed in Ref. 6). In contrast to many other brain functions, conclusions based on primate research must be considered with particular caution when the anatomy and physiology of language processing are concerned. Electrophysiological experiments in primates have implicated both a dorsal and a ventral pathway connecting Wernicke's area to Broca's region (54, 89). Such connections in the human brain have recently been confirmed by using diffusion tensor imaging and tractography (80). A dorsal pathway, including the arcuate fasciculus, was distinguished from a more ventral route, including the external capsule and the uncinate fasciculus. Interestingly, the connections were stronger in the dominant than in the nondominant hemisphere. Although studies on tractography in the human brain do not demonstrate the existence of anatomic, synaptic connectivity, they are indica-

tors of the existence of anatomic pathways between brain areas. The functional connectivity of Broca's region, evident, for example, in covariance analysis of functional magnetic resonance imaging (fMRI), is task specific and much more widely spread than the anatomic connectivity would predict (42). Of course, covarying activation does not necessarily imply a network of directly connected nodes.

Broca's Region with a Mosaic of Functions

Below we briefly discuss various functions that have been ascribed to Broca's region and/or its right-hemisphere counterpart. It should be noted, however, that activation of any area in a brain imaging study does not mean that the neural substrate of the mentioned functions is seated (only) there; rather, it indicates that the activated area is involved in, or may be an important node in, a widely distributed neuronal network. It is most likely that Broca's region consists of partly overlapping subsystems that support various functions, ranging from motor imagery (11, 35) to object manipulation and grasping (13), to motor preparation (59, 90), and to planning (25).

We will proceed from the classical functions of Broca's region in speech production and language to more basic functions in perceptual sequencing, action understanding, and imitation.

Language and speech

In her extensive review of fMRI studies of language areas, Bookheimer (14) showed that areas 44 and 45 subserve different functions. The IFG is often activated bilaterally but shows left-hemispheric dominance during tasks requiring naming (91), judgments of phonology (43, 100), semantics (4, 29, 101), and syntax (9, 28, 29, 43). Broca's region is also activated during acquisition of grammatical rules, discrimination of speech sounds, production of words, estimation of time intervals, and reproduction of rhythms (14). Thus Broca's region seems to be involved in both perception and production of speech. We will claim below that this role of Broca's region as an interface of action and perception can be generalized to nonverbal functions.

Language production and understanding also involve prosody, one of the few language-related processes with right-hemisphere dominance (68, 70). The interaction of the two hemispheres, however, seems to be more complex than has been assumed previously. Integrating evidence from neuroimaging, psycholinguistics, neurology, and neurophysiology, Friederici and Alter (27) proposed that segmental, lexical, and syntactic infor-

mation is processed in different frontotemporal networks in the left hemisphere (including the temporo-parieto-occipital junction, parts of the IFG, and the superior temporal lobe). In contrast, the processing of intonation would be supported by a temporofrontal circuit in the right hemisphere, consisting mainly of the frontal operculum and regions in the superior temporal gyrus. The strict right-hemispheric lateralization of the processing of intonational information can be modulated by stimulus or task demands via the corpus callosum. It was suggested that single regions within the described networks obtain their specific role for the processing of particular aspects of language via interaction with other areas.

Perception-action link for communication: mirror neurons

Communication, both verbal and nonverbal, requires that the interacting individuals "stay tuned." Because the conspecifics certainly are very similar in their main characteristics, it is then also mandatory that each subject's action and perception rely on closely linked neuronal circuitries—one individual's output is the other (similar) individual's input.

Interesting "mirror neurons" were discovered some years ago in frontal area F5 of the monkey cortex. These neurons are active during execution of object-related hand actions, but they are also active, importantly, when the monkey is just observing similar acts (23, 31, 84–86). For example, the mirror neurons are activated when the monkey takes a raisin from a tray and also when he views another monkey or the human experimenter doing the same. No information is yet available about possible hemispheric lateralization of the monkey mirror neurons.

Mirror neurons have visuomotor properties, being sensitive to goal-related motor acts (102), but they can also be activated by sounds that imply actions (55, 57). Importantly, the mirror neurons do not only react to visual input and then project, via some transformational step, to motor-output-related neurons but are also part of a system that forms a neuronal representation of the observed motor acts. Similar to F5, the rostral part of the inferior parietal cortex contains neurons that are active during action observation and execution (32); this region receives input from the STS, which is known to contain neurons responding to biological motion (for review, see Ref. 1).

In search of a human mirror-neuron system (MNS), human counterparts of the monkey mirror neurons were first looked for with PET, which follows oxygen consumption in the brain (40, 59, 86). Broca's region was activated when the subject observed, imagined, and imitated the examiner

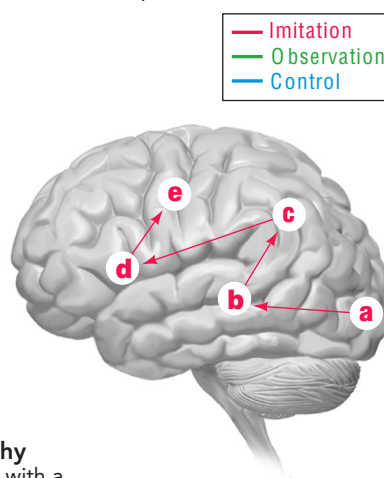
Whole-scalp neuromagnetometer



Nonverbal lip-form stimuli



Activation sequence



Responses

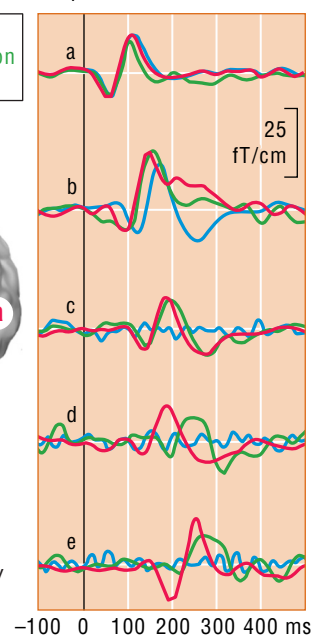


FIGURE 2. Brain activation during imitation studied with magnetoencephalography

Left: magnetoencephalography (MEG) recording with a 306-channel whole scalp neuromagnetometer at the Brain Research Unit, Low Temperature Laboratory, Helsinki University of Technology. MEG picks up weak magnetic fields produced by postsynaptic intracellular currents, arising in synchronously activated cortical pyramidal cells. These magnetic fields, mainly generated by neural currents in fissural cortex, are measured noninvasively outside the head. Right: brain activation by imitation and observation of orofacial gestures. Top shows nonverbal lip forms used as stimuli. Bottom illustrates cortical responses during imitation (red) and observation (green) of nonverbal orofacial gestures. The responses recorded from 5 locations are indicated, and the cortical activation, shown on the schematic brain, progresses from the occipital visual area to the superior temporal sulcus, to the inferior parietal areas, then to Broca's region in the inferior frontal cortex, and finally to the primary motor cortex. Similar activation areas and temporal sequences were seen also in the right hemisphere. The blue traces refer to control stimuli (landscapes that activated only the two first steps). Modified from Ref. 77.

using a precision grasp to enclose an object or to move his/her hand. Thus Broca's region could contain neurons similar to the monkey mirror neurons. The activation sequence associated with online imitation and with observation of another person's movements also included the STS (76, 88).

The monkey F5 mirror neurons are also activated by orofacial gestures, and therefore a recent magnetoencephalography (MEG) study (77) applied still pictures of verbal and nonverbal lip forms that the subject had to observe, imitate, or make in a self-paced manner (FIGURE 2). In all conditions and in both hemispheres, the activation spread from occipital cortex (peak activation 120 ms after the picture onset) in 20- to 60-ms steps to the STS (the strongest activation), the inferior parietal lobule, the inferior frontal lobe (Broca's region), and, 80–100 ms later, to the primary motor cortex. Because the STS is not activated when the subject makes movements his- or herself, it can be consid-

ered only as influencing the (motor) MNS.

Assuming that the observed MNS activation sequence would be related to the link between a sender and a receiver of an action-related message, some abnormalities could be expected in subjects who have abnormal imitation skills and difficulties in understanding motor-act-based intentions of other subjects. Such deficits are observed in high-functioning autistic (Asperger syndrome) subjects, who in fact displayed delayed and diminished activation in Broca's region (75) during imitation (FIGURE 3). Moreover, activation was in many subjects absent in the right hemisphere.

Within the MNS, the close link between perception and action seems to be realized in functions of Broca's region. Such a link may well be important in facilitating communication between an agent and an observer due to shared sensory and motor representations. Along similar lines, Liberman and Mattingly (62) strongly advocated a motor theory of

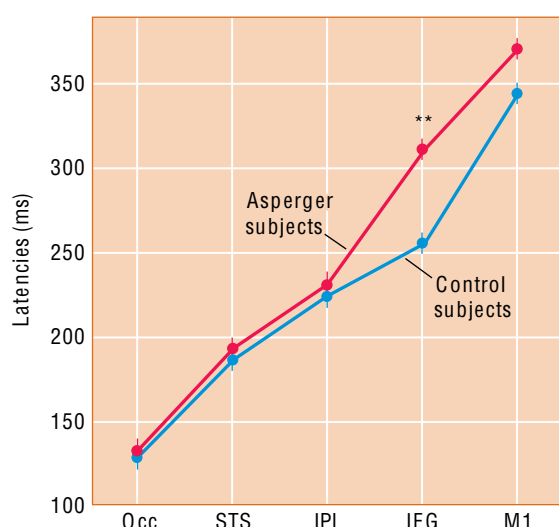


FIGURE 3. Mean peak latencies in the left hemisphere of control subjects and Asperger subjects during imitation of lip forms
There were no significant differences in the duration of the whole activation sequence from the occipital area (Occ) via superior temporal sulcus (STS) to the primary motor cortex (M1) between both groups. The activation interval from the inferior parietal lobule (IPL) to Broca's region (inferior frontal gyrus; IFG) was statistically significantly longer for Asperger subjects than for control subjects; the statistically significant difference is marked with asterisks. Modified from Ref. 75.

speech, meaning that the listener perceives the speech sounds in terms of how they are articulated rather than in terms of their acoustic characteristics.

In line with left-hemisphere control for speech, orofacial gestures show a right hemimouth dominance in babies during babbling, as opposed to smiling (45). Corresponding results have been observed in humans (McGurk effect attenuated when the speaker's right hemimouth is covered; Ref. 74) and in marmosets (right hemimouth dominance for social contact calls as opposed to expressions of negative emotion; Ref. 46).

An action-perception link seems especially important during language acquisition: when the child listens to a new word, s/he automatically tries to imitate it, thereby forming a close temporal link between sensing (hearing) and acting (articulating). Language acquisition through imitation of speech sounds could well be supported by the acoustic mirror neurons in F5/Broca's region (57, 83). The close connection between speech perception and imitation/production becomes manifest also in adults when they modify their accent and syntax according to the speaker with whom they are interacting.

In a combined transcranial magnetic stimulation (TMS) and PET study, auditory speech activated the left IFG, suggesting that this area primes the motor system to respond to heard speech (103), one more hint for a role of Broca's area as an inter-

face between perception and action.

A role of area 44/45 as an interface between perception and action is also suggested by the inhibitory influence of right IFG on certain imitative and overlearned responses (Ref. 15; see Ref. 7 for more general inhibitory functions of right IFG).

To sum up, mirror neurons, as important parts of larger neuronal circuitries, can be considered to transfer action-related information (be it visual or auditory) to knowledge (83). The available information is in line with the view that the MNS supports communicative functions. STS and inferior parietal cortex provide essential input to F5/Broca's region, where the communicative functions of the MNS become manifest.

Action understanding

Rizzolatti and co-workers (83, 87, 88) consider Broca's region essential for action understanding. Support for such an idea comes from studies in which monkey F5 neurons also react when the end part of the movement is obscured when the monkey only knows what is going to happen (102). Furthermore, a part of the F5 mirror neurons are also activated by sounds that are related to actual motor acts and the monkey understands this relationship (57).

Observation of different types of mouth actions activates several brain areas, including the pars opercularis of the IFG and the adjacent ventral premotor cortex, with different patterns and likely via different mechanisms influenced by knowledge of the observed action (12, 17). Interestingly, Broca's region was not activated when the human subjects watched a dog barking, i.e., an action that is not in the observer's motor repertoire (17). In addition to Broca's region and premotor cortex, the primary motor cortex also shows differential activation dependent on action understanding: MEG results about the motor-cortex part of the human MNS suggest that the motor cortex differentiates natural and artificially presented movements (52). Moreover, a recent study of observation of chopstick use demonstrated that the motor cortex is activated more strongly the more often the (Finnish) subjects had used chopsticks during the last year. In other words, a dependence on experience was demonstrated in the motor-cortex part of the MNS (53).

Humans most likely understand another person's actions, and also their motor-act-based intentions, by mapping observed actions, postures, and gaze onto their own motor representations of similar actions. The observed motor sequence may evoke memories and experiences of motor patterns performed earlier. If the observed motor sequence contains recognizable parts that already are included in the observer's own motor vocabulary, it is far

easier to both understand and imitate the new sequence.

Imitation

As a part of the human MNS, Broca's region seems to have an important role in imitation, a capability different from direct copying of the action without understanding its goal. "True" imitation relies on perception-action coupling and allows the imitator to perform totally new motor actions, thereby forming the basis for skill learning (67). In true imitation, the observed motor patterns are directly matched on the observer's own internal motor representations; this is a fundamentally different mechanism from detailed visual analysis, followed by matching of the visual and motor reference frames.

The role of Broca's region in imitation is still under debate; a recent study claimed that most of the previous studies have had too little variability in the imitated actions so that the imitator could have just kept in mind the limited set of movement patterns, repeating them as well as if they were coded with numbers (64). Another possible contaminating factor in studies reporting activation in Broca's region could be covert verbalization ("internal speech") during the motor acts.

In an fMRI study, imitation of action strongly involved the left IFG (49). Imitation of goal-directed actions (as compared with non-goal-directed actions) led to more intense activation of the bilateral IFG (58). In an extensive analysis of seven fMRI studies, Molnar-Szakacs et al. (71) concluded that Broca's region is functionally parcellated so that imitation-related activation occurs at the dorsal and ventral part of the pars opercularis, whereas the pars triangularis is activated only during observation and not during imitation. Accordingly, MEG recordings showed stronger responses of Broca's region (and of the primary motor cortex) during imitation than action observation or execution (75–77); the reason may be either facilitation/enhancement of responses by imitation or the coactivation and summing-up of two different neuronal populations.

As further support for the importance of the IFG in imitation, fMRI activation was stronger during imitation than during simple observation of facial expressions in the IFG, the superior temporal cortex, insula, and amygdala (20), and imitation—but not execution—of finger movements was impaired during repetitive TMS applied over the left and right pars opercularis (44).

Some action patterns are highly contagious. For example, watching another person yawn may trigger the viewer to do the same. In an fMRI study in which subjects watched videotaped yawns vs. non-nameable, nonyawn facial gestures, no yawn-spe-

cific activation was observed in Broca's region (98). Thus activation associated with yawn contagiousness seems not to rely on essential parts of the MNS, in line with the nature of contagious yawns as automatically released behavioral acts rather than a truly imitated motor pattern that would require detailed action understanding.

Proponents of the ideomotor theory have noted, as early as the 19th century, that an idea leads to an action, unless it is actively suppressed. Although some of us can view a cold beer on the table without drinking it, patients with frontal lobe lesions may display echoing behavior so that perception leads to an automatic response (61). In healthy subjects, some spinal mechanisms are inhibited at the same time as facilitation occurs at the cortical level (8).

Forward and inverse models

Planning an action, for example reaching for an object, includes expectation of the sensory consequences. "Forward models," considered to underlie such predictions, are thought to involve efference copies that inform the sensory brain areas about the forthcoming sensory input, which then would be compared with the predictions. For example, utterances deviating infrequently from the frequently produced vowels do not elicit change-related responses in the human auditory cortex although the same sounds presented externally (from tape) do so (22). "Inverse models," on the other hand, refer to (e.g., visual) feedback from movements that are needed to reach the object.

Broca's region has been suggested as an interface between inverse and forward models (48), coding the goal of an action (in the dorsal part) and also sending efference copies to the STS (in the ventral part). Specifically, Broca's region would receive visual input from the STS via the parietal cortex and would process it into action plans. A competing hypothesis stresses the role of the posterior parietal cortex as the interface between inverse and forward models (69). The forward and inverse models are useful in conceptualizing sequences of brain activation during online imitation of another person's actions.

It is interesting that the inverse and forward models propose activation sequences very similar to those that have already been demonstrated (for the inverse model case) with MEG; for example, **FIGURE 2** pinpointed dynamic activation from the STS to inferior parietal cortex, Broca's region, and finally to the primary motor cortex (77).

Motor and perceptual sequencing

Parsing is essential for understanding any observed actions and for their consequent imitation. Think

for example how while learning a new language we first face great difficulties in segmenting the message into single words. Broca's region could have a role in action segmentation (on the sensory side) and in action sequencing (on the motor side). In support of such a role in representing sequential information, Broca's region is activated during auditory and visual rhythm-monitoring tasks (93) and during attention to timing and speed of moving objects, as opposed to attention to properties of the objects (94–96). Interestingly, IFG is activated by sequences of biological stimuli (such as goal-directed motion) but not during completion of geometric figure sequences (97). Deviation from an expected sequence may explain why Broca's region and its right-hemisphere counterpart are activated when musical syntax is violated (63).

Brain-damage data suggest that hemispheres might have different roles in sequencing: Left-hemisphere lesions preferably affect verbal sequencing, and right-hemisphere lesions affect nonverbal sequencing (14, 56).

Hand gestures and their relation to speech

Speech production and speech-related gestures are connected to such a degree that they have been considered as outlets of the same thought process (39), a view supported by the finding that hand and orofacial gestures are supported by the speech production area, i.e., Broca's region.

Speech-related gestures may occur even when the speaker-gesturer knows that others cannot see the gestures, e.g., during a phone call. Similarly, congenitally blind persons may also gesture when speaking with other blind people (38, 50). The close connections between speech production and hand gestures are also supported by studies of hearing babies born to deaf parents: the infants' hand actions display a similar rhythm to babbling (81). In stutterers, speech-related hand gestures freeze at the same time as the speech is disturbed; however, non-speech-related hand movements can continue normally (66). Along similar lines, observation of grasping movements can influence the observer's simultaneous mouth movements and syllable pronunciation (33, 34).

All of these findings suggest an intimate connection between speech-related hand and face gestures and the production of speech. The corepresentation of speech and gestures in Broca's region could reflect shared evolutionary roots. Accordingly, Rizzolatti and Arbib (82) suggested that hand and orofacial gestures—rather than primate vocalizations—are the precursors of human language; their proposal links earlier gestural theories to recent neurophysiological results about the MNS. The close connection between gestures and

speech/language is also evident from the spontaneous emergence of sign languages in isolated societies of deaf persons (99) and of the brain-imaging findings that sign language activates very similar brain regions to those activated by speech (47, 60). Interestingly, Horwitz et al. (47) showed an extensive involvement of area 45 in spoken and signed language, suggesting representation of modality-independent aspects of language generation in the inferior frontal cortex.

Broca's Region: Conclusions and Speculations

Broca's region encompassing Brodmann's cytoarchitectonic areas 44 and 45 in the left hemisphere, with representations of face, head, and hands—but not of foot—may have evolved into a special communication area relying on orofacial gestures and hand movements. That function requires representation and segmentation of rapidly changing motor and sensory patterns and a close matching of these two to form an action-perception interface.

Far beyond its classical language functions, Broca's region contributes to action planning, action observation, action understanding, and imitation. Speech production and comprehension can be considered a highly developed form of action execution/observation matching (see also the motor theory of speech; Ref. 62). The new concepts of “motor cognition” (51) and “sequential cognition” (24) may be useful as first approximations of the wide range of functions subserved by Broca's region.

The role of Broca's region in action understanding, derived from findings of mirror-neuron research, is also supported by the following observations:

- 1) when subjects view and listen to speaking faces, activation of Broca's region is stronger during incongruent than during congruent audiovisual stimuli (79);
- 2) when dyslexic subjects passively view words, they show stronger Broca's region activation than do normal-reading subjects (92); and
- 3) when patients with cochlear prosthesis listen to their native language, they show stronger Broca's region activation than do normal-hearing subjects (72).

In all of these conditions, Broca's region seems to be more strongly activated when the task requires much effort for understanding the sensory message.

As a likely interface for sensory and motor sequencing, Broca's region is in a good position to

support action understanding in general. True imitation can follow only when the action is first parsed and understood. Strong effort for action understanding also recruits top-down influences based on the subject's previous experience, and thus predictive behavior can result (26).

The studies reviewed here converge on a central role of Broca's region as an orchestrator of time-sensitive perceptual and motor functions underlying verbal and nonverbal communication. However, several questions still remain open, such as whether and how specific language functions (e.g., those related to syntax; cf. Refs. 10 and 41) have common evolutionary roots with the perceptual and motor functions supported by Broca's region and to what extent their neuronal correlates overlap. Once the basic functions and neuronal substrates are identified, information is also needed about temporal activation sequences and connectivity to fully unravel the multitude of brain functions to which Broca's region contributes. ■

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