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伊藤和幸，湯下和雄	画像処理を利用したマウスポインティングデバイスの開発について	信学技報	105	39-43	2005
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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.

Nobuyuki Nishitani,[1] Martin Schürmann,[2] Katrin Amunts,[3] and Riitta Hari[2,4]

[1]Cognitive Functions Section, Department of Rehabilitation for Sensory Functions, Research Institute, National Rehabilitation Centre for Persons with Disabilities, Tokorozawa, Japan; [2]Brain Research Unit, Low Temperature Laboratory, Helsinki University of Technology, Espoo, Finland; [3]Institute of Medicine, Forschungszentrum Jülich, Jülich, Germany; and [4]Department of Clinical Neurophysiology, University of Helsinki, Helsinki, Finland
hari@neuro.hut.fi

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
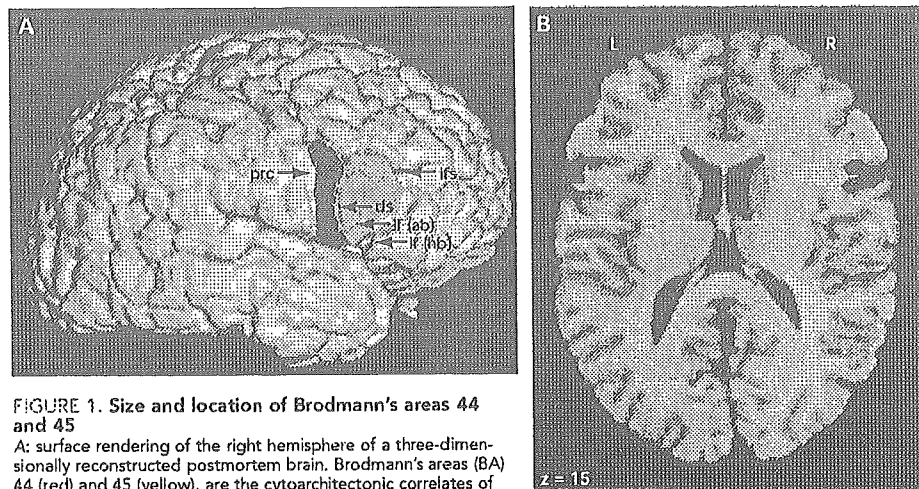
FIGURE 1. Size and location of Brodmann's areas 44 and 45
A: surface rendering of the right hemisphere of a three-dimensionally reconstructed postmortem brain. Brodmann's areas (BA) 44 (red) and 45 (yellow), are the cytoarchitectonic correlates of of Broca's region and are its right-hemispheric homolog. 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.
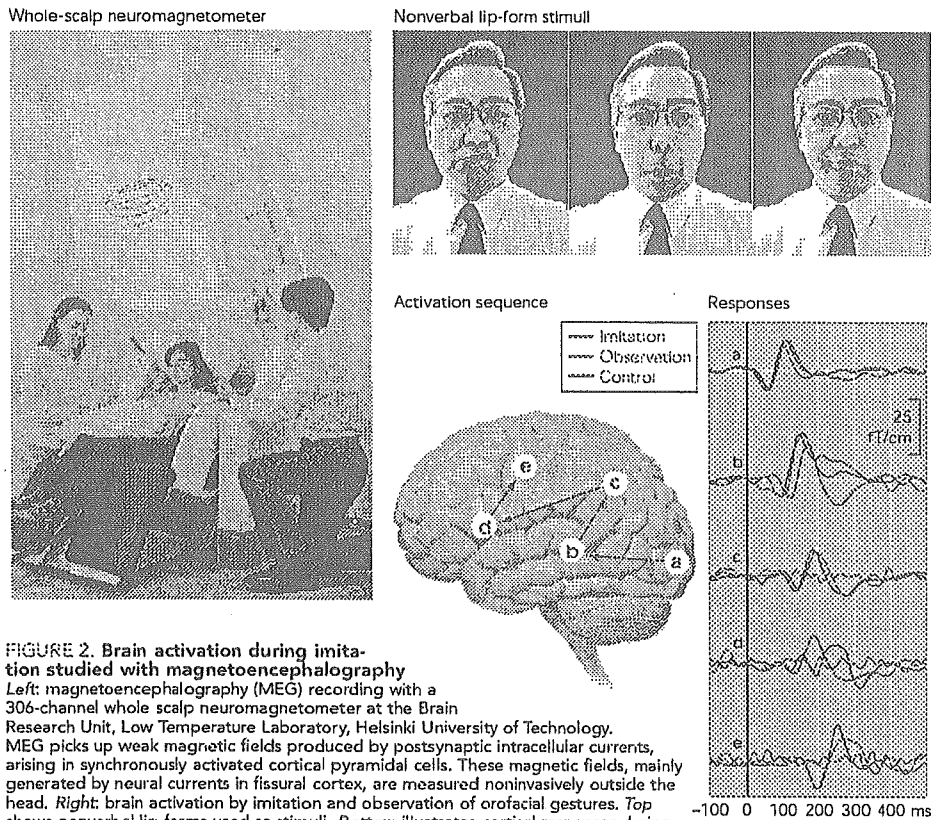
Perception-action link for communication: mirror neurons

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

- Imitation
- Observation
- Control

-100 0   100 200 300 400 ms

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 considered 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
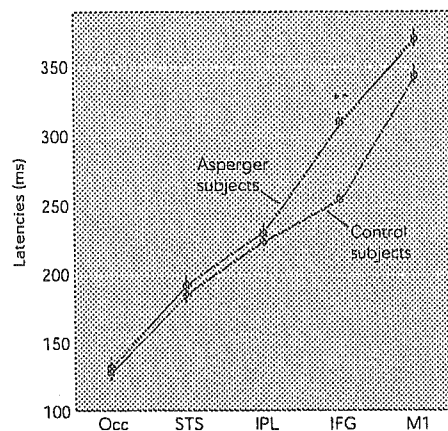
FIGURE 3. Mean peak latencies in the left hemisphere of control subjects and Asperger subjects during imitation of lip forms
There were no significant differences in the duration of the whole activation sequence from the occipital area (Occ) via superior temporal sulcus (STS) to the primary motor cortex (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. ▩

References

1. Allison T, Puce A, and McCarthy G. Social perception from visual cues: role of the STS region. *Trends Cogn Sci* 4: 267–278, 2000.

2. Amunts K, Schleicher A, Bürgel U, Mohlberg H, Uylings HB, and Zilles K. Broca's region revisited: cytoarchitecture and intersubject variability. *J Comp Neurol* 412: 319–341, 1999.

3. Amunts K, Schleicher A, Ditterich A, and Zilles K. Broca's region: cytoarchitectonic asymmetry and developmental changes. *J Comp Neurol* 465: 72–89, 2003.

4. Amunts K, Weiss PH, Mohlberg H, Pieperhoff P, Eickhoff S, Gurd JM, Marshall JC, Shah NJ, Fink GR, and Zilles K. Analysis of neural mechanisms underlying verbal fluency in cytoarchitectonically defined stereotaxic space—the roles of Brodmann areas 44 and 45. *Neuroimage* 22: 42–56, 2004.

5. Amunts K and Zilles K. Advances in cytoarchitectonic mapping of the human cerebral cortex. *Neuroimaging Clin N Am* 11: 151–169, 2001.

6. Arbib M and Bota M. Language evolution: neural homologies and neuroinformatics. *Neural Netw* 16: 1237–1260, 2003.

7. Aron AR, Robbins TW, and Poldrack RA. Inhibition and the right inferior frontal cortex. *Trends Cogn Sci* 8: 170–177, 2004.

8. Baldissera F, Cavallari P, Craighero L, and Fadiga L. Modulation of spinal excitability during observation of hand actions in humans. *Eur J Neurosci* 13: 190–194, 2001.

9. Ben-Shachar M, Hendler T, Kahn I, Ben-Bashat D, and Grodzinsky Y. The neural reality of syntactic transformations: evidence from functional magnetic resonance imaging. *Psychol Sci* 14: 433–440, 2003.

10. Ben-Shachar M, Palti D, and Grodzinsky Y. Neural correlates of syntactic movement: converging evidence from two fMRI experiments. *Neuroimage* 21: 1320–1336, 2004.

11. Binkofski F, Amunts K, Stephan KM, Posse S, Schormann T, Freund HJ, Zilles K, and Seitz RJ. Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Hum Brain Mapp* 11: 273–285, 2000.

12. Binkofski F and Buccino G. Motor functions of the Broca's region. *Brain Lang* 89: 362–369, 2004.

13. Binkofski F, Buccino G, Stephan KM, Rizzolatti G, Seitz RJ, and Freund HJ. A parieto-premotor network for object manipulation: evidence from neuroimaging. *Exp Brain Res* 128: 210–213, 1999.

14. Bookheimer S. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu Rev Neurosci* 25: 151–188, 2002.

15. Brass M, Derrfuss J, and von Cramon DY. The inhibition of imitative and overlearned responses: a functional double dissociation. *Neuropsychologia* 43: 89–98, 2005.

16. Brodmann K. *Vergleichende Lokalisationslehre der Großhirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues.* Leipzig: Johann Ambrosius Barth, 1909.

17. Buccino G, Lui F, Canessa N, Patteri I, Lagravinese G, Benuzzi F, Porro CA, and Rizzolatti G. Neural circuits involved in the recognition of actions performed by nonconspecifics: an fMRI study. *J Cogn Neurosci* 16: 114–126, 2004.

18. Cantalupo C and Hopkins WD. Asymmetric Broca's area in great apes. *Nature* 414: 505, 2001.

19. Caplan D. *Language: Structure, Processing, and Disorders.* Cambridge, MA: Massachusetts Institute of Technology Press, 1996.

20. Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, and Lenzi GL. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci USA* 100: 5497–5502, 2003.

21. Corballis MC. From mouth to hand: gesture, speech, and the evolution of right-handedness. *Behav Brain Sci* 26: 199–208, 2003.

22. Curio G, Neuloh G, Numminen J, Jousmäki V, and Hari R. Speaking modifies voice-evoked activity in the human auditory cortex. *Hum Brain Mapp* 9: 183–191, 2000.

23. Di Pellegrino G, Fadiga L, Fogassi L, Gallese V, and Rizzolatti G. Understanding motor events: a neurophysiological study. *Exp Brain Res* 91: 176–180, 1992.

24. Dominey PF, Hoen M, Blanc JM, and Lelekov-Boissard T. Neurological basis of language and sequential cognition: evidence from simulation, aphasia, and ERP studies. *Brain Lang* 86: 207–225, 2003.

25. Fincham JM, Carter CS, van Veen V, Stenger VA, and Anderson JR. Neural mechanisms of planning: a computational analysis using event-related fMRI. *Proc Natl Acad Sci USA* 99: 3346–3351, 2002.

26. Flanagan JR and Johansson RS. Action plans used in action observation. *Nature* 424: 769–771, 2003.

27. Friederici AD and Alter K. Lateralization of auditory language functions: a dynamic dual pathway model. *Brain Lang* 89: 267–276, 2004.

28. Friederici AD and Kotz SA. The brain basis of syntactic processes: functional imaging and lesion studies. *Neuroimage* 20, Suppl 1: S8–S17, 2003.

29. Friederici AD, Rüschemeyer SA, Hahne A, and Fiebach CJ. The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cereb Cortex* 13: 170–177, 2003.

30. Galaburda AM. La région de Broca: observations anatomiques faites un siècle apres la mort de son découvreur. *Rev Neurol (Paris)* 136: 609–616, 1980.

31. Gallese V, Fadiga L, Fogassi L, and Rizzolatti G. Action recognition in the premotor cortex. *Brain* 119: 593–609, 1996.

32. Gallese V, Fogassi L, Fadiga L, and Rizzolatti G. Action representation and the inferior parietal lobule. In: *Attention & Performance XIX. Common Mechanisms in Perception and Action,* edited by Prinz W and Hommel B. Oxford: Oxford University Press, 2002.

33. Gentilucci M. Grasp observation influences speech production. *Eur J Neurosci* 17: 179–184, 2003.

34. Gentilucci M, Benuzzi F, Gangitano M, and Grimaldi S. Grasp with hand and mouth: a kinematic study on healthy subjects. *J Neurophysiol* 86: 1685–1699, 2001.

35. Gerardin E, Sirigu A, Lehericy S, Poline JB, Gaymard B, Marsault C, Agid Y, and Le Bihan D. Partially overlapping neural networks for real and imagined hand movements. *Cereb Cortex* 10: 1093–1104, 2000.

36. Glynn L. *An Anatomy of Thought. The Origin and Machinery of the Mind.* Oxford: Oxford University Press, 1999.

37. Gogtay N, Giedd JN, Lusk L, Hayashi KM, Greenstein D, Vaituzis AC, Nugent TF 3rd, Herman DH, Clasen LS, Toga AW, Rapoport JL, and Thompson PM. Dynamic mapping of human cortical development during childhood through early adulthood. *Proc Natl Acad Sci USA* 101: 8174–8179, 2004.

— 30 —

38. Goldin-Meadow S. The resilience of language. New York: Psychology Press, 2003.

39. Goldin-Meadow S. The role of gesture in communication and thinking. Trends Cogn Sci 3: 419–429, 1999.

40. Grafton ST, Arbib MA, Fadiga L, and Rizzolatti G. Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. Exp Brain Res 112: 103–111, 1996.

41. Grodzinsky Y. The neurology of syntax: language use without Broca's area. Behav Brain Sci 23: 1–71, 2000.

42. He AG, Tan LH, Tang Y, James GA, Wright P, Eckert MA, Fox PT, and Liu Y. Modulation of neural connectivity during tongue movement and reading. Hum Brain Mapp 18: 222–232, 2003.

43. Heim S, Opitz B, and Friederici AD. Distributed cortical networks for syntax processing: Broca's area as the common denominator. Brain Lang 85: 402–408, 2003.

44. Heiser M, Iacoboni M, Maeda F, Marcus J, and Mazziotta JC. The essential role of Broca's area in imitation. Eur J Neurosci 17: 1123–1128, 2003.

45. Holowka S and Petitto LA. Left hemisphere cerebral specialization for babies while babbling. Science 297: 1515, 2002.

46. Hook-Costigan MA and Rogers LJ. Lateralized use of the mouth in production of vocalizations by marmosets. Neuropsychologia 36: 1265–1273, 1998.

47. Horwitz B, Amunts K, Bhattacharyya R, Patkin D, Jeffries K, Zilles K, and Braun AR. Activation of Broca's area during the production of spoken and signed language: a combined cytoarchitectonic mapping and PET analysis. Neuropsychologia 41: 1868–1876, 2003.

48. Iacoboni M, Kaplan J, and Wilson S. A neural architecture for imitation and intentional relations. In: Imitation and Social Learning in Robots, Humans, and Animals: Behavioural, Social and Communicative Dimensions, edited by Nehaniv C and Dautenhahn K. Cambridge, UK: Cambridge University Press. In press.

49. Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, and Rizzolatti G. Cortical mechanisms of human imitation. Science 286: 2526–2528, 1999.

50. Iverson JM and Goldin-Meadow S. Why people gesture when they speak. Nature 396: 228, 1998.

51. Jackson PL and Decety J. Motor cognition: a new paradigm to study self-other interactions. Curr Opin Neurobiol 14: 259–263, 2004.

52. Järveläinen J, Schürmann M, Avikainen S, and Hari R. Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. Neuroreport 12: 3493–3495, 2001.

53. Järveläinen J, Schürmann M, and Hari R. Activation of the human primary motor cortex during observation of tool use. Neuroimage 23: 187–192, 2004.

54. Kaas JH and Hackett TA. 'What' and 'where' processing in auditory cortex. Nat Neurosci 2: 1045–1047, 1999.

55. Keysers C, Kohler E, Umiltà MA, Nanetti L, Fogassi L, and Gallese V. Audiovisual mirror neurons and action recognition. Exp Brain Res 153: 628–636, 2003.

56. Kim Y, Royer F, Bonstelle C, and Boller F. Temporal sequencing of verbal and nonverbal materials: the effect of laterality of lesion. Cortex 16: 135–143, 1980.

57. Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, and Rizzolatti G. Hearing sounds, understanding actions: action representation in mirror neurons. Science 297: 846–848, 2002.

58. Koski L, Wohlschläger A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, and Iacoboni M. Modulation of motor and premotor activity during imitation of target-directed actions. Cereb Cortex 12: 847–855, 2002.

59. Krams M, Rushworth MF, Deiber MP, Frackowiak RS, and Passingham RE. The preparation, execution and suppression of copied movements in the human brain. Exp Brain Res 120: 386–398, 1998.

60. Levänen S, Uutela K, Salenius S, and Hari R. Cortical representation of sign language: comparison of deaf signers and hearing non-signers. Cereb Cortex 11: 506–512, 2001.

61. Lhermitte F. 'Utilization behaviour' and its relation to lesions of the frontal lobes. Brain 106: 237–255, 1983.

62. Liberman AM and Mattingly IG. The motor theory of speech perception revised. Cognition 21: 1–36, 1985.

63. Maess B, Koelsch S, Gunter TC, and Friederici AD. Musical syntax is processed in Broca's area: an MEG study. Nat Neurosci 4: 540–545, 2001.

64. Makuuchi M. Is Broca's area crucial for imitation? Cereb Cortex. In press.

65. Matelli M and Luppino G. Functional anatomy of human motor cortical areas. In: Handbook of Neuropsychology, edited by Boller F and Grafman J. Amsterdam: Elsevier, 1997, p. 9–26.

66. Mayberry RI and Jacques J. Gesture production during stuttered speech: insights into the nature of gesture-speech integration. In: Language and Gesture, edited by McNeill D. Cambridge, UK: Cambridge University Press, 2000, p. 199–214.

67. Meltzoff AN and Decety J. What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. Philos Trans R Soc Lond B Biol Sci 358: 491–500, 2003.

68. Meyer M, Alter K, Friederici AD, Lohmann G, and von Cramon DY. FMRI reveals brain regions mediating slow prosodic modulations in spoken sentences. Hum Brain Mapp 17: 73–88, 2002.

69. Miall RC. Connecting mirror neurons and forward models. Neuroreport 14: 2135–2137, 2003.

70. Mitchell RL, Elliott R, Barry M, Cruttenden A, and Woodruff PW. The neural response to emotional prosody, as revealed by functional magnetic resonance imaging. Neuropsychologia 41: 1410–1421, 2003.

71. Molnar-Szakacs I, Iacoboni M, Koski L, and Mazziotta J. Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. Cereb Cortex. In press.

72. Naito Y, Okazawa H, Honjo I, Takahashi H, Kawano M, Ishizu K, and Yonekura Y. Cortical activation during sound stimulation in cochlear implant users demonstrated by positron emission tomography. Ann Otol Rhinol Laryngol Suppl 166: 60–64, 1995.

73. Nakamura K, Kawashima R, Ito K, Sugiura M, Kato T, Nakamura A, Hatano K, Nagumo S, Kubota K, Fukuda H, and Kojima S. Activation of the right inferior frontal cortex during assessment of facial emotion. J Neurophysiol 82: 1610–1614, 1999.

74. Nicholls ME, Searle DA, and Bradshaw JL. Read my lips: asymmetries in the visual expression and perception of speech revealed through the McGurk effect. Psychol Sci 15: 138–141, 2004.

75. Nishitani N, Avikainen S, and Hari R. Abnormal imitation-related cortical activation sequences in Asperger's syndrome. Ann Neurol 55: 558–562, 2004.

76. Nishitani N and Hari R. Temporal dynamics of cortical representation for action. Proc Natl Acad Sci USA 97: 913–918, 2000.

77. Nishitani N and Hari R. Viewing lip forms: cortical dynamics. Neuron 36: 1211–1220, 2002.

78. Nomura M, Iidaka T, Kakehi K, Tsukiura T, Hasegawa T, Maeda Y, and Matsue Y. Frontal lobe networks for effective processing of ambiguously expressed emotions in humans. Neurosci Lett 348: 113–116, 2003.

79. Ojanen V, Möttönen R, Pekkola J, Jääskeläinen IP, and Sams M. Processing of audiovisual speech in the Broca's area. Under revision.

80. Parker GJM, Luzzi S, Alexander DC, Wheeler-Kingshott CAM, Ciccarelli O, and Lambon Ralph MA. Lateralization of ventral and dorsal auditory-language pathways in the human brain. Neuroimage. In press.

81. Petitto LA, Holowka S, Sergio LE, and Ostry D. Language rhythms in baby hand movements. Nature 413: 35–36, 2001.

82. Rizzolatti G and Arbib MA. Language within our grasp. Trends Neurosci 21: 188–194, 1998.

83. Rizzolatti G and Craighero L. The mirror-neuron system. Annu Rev Neurosci 27: 169–192, 2004.

84. Rizzolatti G, Fadiga L, Fogassi L, and Gallese V. Resonance behaviors and mirror neurons. Arch Ital Biol 137: 85–100, 1999.

85. Rizzolatti G, Fadiga L, Gallese V, and Fogassi L. Premotor cortex and the recognition of motor actions. Brain Res Cogn Brain Res 3: 131–141, 1996.

86. Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, and Fazio F. Localization of grasp representations in humans by PET: 1. Observation versus execution. Exp Brain Res 111: 246–252, 1996.

87. Rizzolatti G, Fogassi L, and Gallese V. Motor and cognitive functions of the ventral premotor cortex. Curr Opin Neurobiol 12: 149–154, 2002.

88. Rizzolatti G, Fogassi L, and Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2: 661–670, 2001.

89. Romanski LM, Tian B, Fritz JB, Mishkin M, Goldman-Rakic PS, and Rauschecker JP. Reply to "'What', 'where' and 'how' in auditory cortex'." Nat Neurosci 3: 966, 2000.

90. Rushworth MF, Krams M, and Passingham RE. The attentional role of the left parietal cortex: the distinct lateralization and localization of motor attention in the human brain. J Cogn Neurosci 13: 698–710, 2001.

91. Salmelin R, Hari R, Lounasmaa OV, and Sams M. Dynamics of brain activation during picture naming. Nature 368: 463–465, 1994.

92. Salmelin R, Service E, Kiesilä P, Uutela K, and Salonen O. Impaired visual word processing in dyslexia revealed with magnetoencephalography. Ann Neurol 40: 157–162, 1996.

93. Schubotz RI, Friederici AD, and von Cramon DY. Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI. Neuroimage 11: 1–12, 2000.

94. Schubotz RI and von Cramon DY. A blueprint for target motion: fMRI reveals perceived sequential complexity to modulate premotor cortex. Neuroimage 16: 920–935, 2002.

95. Schubotz RI and von Cramon DY. Functional organization of the lateral premotor cortex: fMRI reveals different regions activated by anticipation of object properties, location and speed. Brain Res Cogn Brain Res 11: 97–112, 2001.

— 31 —

96. Schubotz RI and von Cramon DY. Predicting perceptual events activates corresponding motor schemes in lateral premotor cortex: an fMRI study. Neuroimage 15: 787–796, 2002.

97. Schubotz RI and von Cramon DY. Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. J Neurosci 24: 5467–5474, 2004.

98. Schürmann M, Hesse MD, Stephan KE, Saarela M, Zilles K, Hari R, and Fink GR. Yearning to yawn: the neural basis of contagious yawning. Neuroimage. In press.

99. Senghas A, Kita S, and Ozyurek A. Children creating core properties of language: evidence from an emerging sign language in Nicaragua. Science 305: 1779–1782, 2004.

100. Thierry G, Boulanouar K, Kherif F, Ranjeva JP, and Démonet JF. Temporal sorting of neural components underlying phonological processing. Neuroreport 10: 2599–2603, 1999.

101. Thompson-Schill SL, D'Esposito M, Aguirre GK, and Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc Natl Acad Sci USA 94: 14792–14797, 1997.

102. Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, and Rizzolatti G. I know what you are doing. A neurophysiological study. Neuron 31: 155–165, 2001.

103. Watkins K and Paus T. Modulation of motor excitability during speech perception: the role of Broca's area. J Cogn Neurosci 16: 978–987, 2004.

脳磁図による
脳機能の解明

国立身体障害者リハビリテーションセンター研究所
感覚機能系障害研究部感覚認知障害研究室室長

西谷信之
Nishitani Nobuyuki
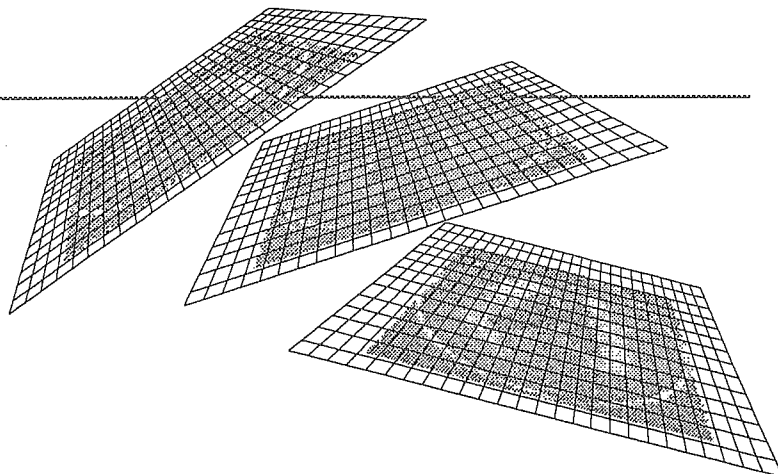
脳磁場の主な発生源は、大脳皮質錐体細胞の尖樹状突起内に誘発される興奮性後シナプス電位の変化による細胞内電流であると考えられている。この細胞内電流の周囲に、右ねじの法則に従って発生する磁場を計測している(図1)。ほとんどの脳磁場計測装置(magnetoencephalography：MEG)は、脳表に平行な尖樹状突起内の細胞内電流が形成する垂直方向の磁場成分を記録するのに対して、脳波は脳表に対して垂直水平両方向の細胞内電流を計測することから、両者は相補的な関係にあると考えられる。

脳磁図(magnetoencephalogram：MEG)計測の基礎研究は、1960年ころより始められたが、当初計測チャンネルの少ない磁場計測装置であったために、脳全域からの同時記録が不可能であった。また、地磁場に比べて約10億分の1程度と非常に微弱なために、安定した脳磁場の計測が困難であった。しかしその後1970年代に入り、極低温下における超伝導技術を用いた超伝導量子干渉素子(superconducting quantum interference device：SQUID)が開発され、磁場計測が実用されるようになった。さらに計測コイルの多様化と、チャンネル数が増加し、現在ではほぼ頭部全体を覆う多チャンネル脳磁場計測装置が開発されている(図2、3、p14)。

脳磁場計測の特徴は、優れた時間・空間分解能にある。1ミリ秒のレベルで複数の脳活動部位の時間的関係を明らかにすることが出来る。また、頭蓋骨・脳脊髄液・脳・硬膜などの頭部の構成組織の透磁率は均一とみなされるために、頭部術後や頭部挫傷後などの構成組織の変化による頭皮上の磁場信号とその分布には歪みが生じない。その結果、計測された磁場信号に基づく脳内活動源を数mm以内の誤差で推定することが出来る。また活動の大きさは、脳波のような基準電極との相対値ではなく、絶対値として求められる。

MEGを用いて、認知・記憶・言語等の高次脳機能に関して、多くの基礎および臨床研究が実施されてきた。さらに最近社会的要請により、びまん性軸索損傷に代表されるような、構造学的に著明な変化のない症例での認知障害などの高次脳機能の解明にも応用されている。本稿では、近年のMEGによる脳機能解明の一部を紹介する。

随意脳活動

近年最も臨床応用がなされているのは、てんかんの発作波の活動源推定であり、特に難治性側頭葉てんかんの海馬、偏頭核部分切除術に対する、てんかん源性発作焦点の術前診断の手法として重要な役割を担っている。一方、随意脳活動のひとつとして、睡眠時第2段階に認められる紡錘波の発生機序の解明にも応用されている。図4(p14)は、14 Hz中心頭頂紡錘波の頭皮上脳波と脳磁場の同時記録である。頭皮上脳波と同じ周波数帯域の紡錘波を、脳磁場計測でも両側半球に認める。この大脳皮質内活動源は、両側半球の中心溝の前後に求められる。一方、視床などの深部発生源も同定されているが、頭皮上に認められる紡錘波の発生に、どのように深部構造がかかわっているかの解明は、今後の課題となっている。

高次視聴覚機能

視覚系の磁場応答に関するMEGの応用も多くなされている。このなかで視覚系高次機能の障害には、幻視、変形視、色覚障害等々が存在するが、ここでは相貌失認(prosopagnosia)、半側空間無視(unilateral spatial neglect / hemispatial neglect)について述べる。相貌失認は、身近な人や有名でよく知っているはずの人々の顔が識別できないのに対して、声・服装・髪型などの特徴により、だれであるか

を認知できる病態である。その主病巣部位は後側頭葉下内側部(fusiform gyrus)、特に右側にあるといわれている[1]。MEGでの研究では、顔写真の刺激後約120〜160ミリ秒前後でfusiform gyrusに活動を認めており、深部電極記録と一致した結果が得られている[2]。半側空間無視は刺激に対する反応や行動において、感覚や運動障害が存在しないのにもかかわらず、大脳病巣の反対側の刺激や空間に気付かない病態である。右半球頭頂葉が主責任病巣と考えられている[3]。この頭頂部は視覚運動統合機構において、視線・四肢追視運動制御の中心部位であることから、頭頂部の活動の程度を明らかにすることで、半側空間無視の病態の評価が可能であると考えられる(図5、p14)[4]。

一方、刺激音の周波数と一次聴覚野の推定発生源の位置との関係では、周波数が高くなるに従い推定電流源は深くなることがわかっている(spatial tonotopy)。このことは、閾値レベルの刺激においても保たれて、音刺激消失後数秒間持続する聴覚残像においても同様なspatial tonotopyが認められる。一方、耳鳴りの存在する耳とは対側の一次聴覚野においては、健常者に認められるspatial tonotopyが耳鳴りに対応した周波数で逸脱しており(図6、p15)[5]、聴覚野における可塑的変化と考えられ、耳鳴りの臨床診断と治療に活用されることが期待される。

注意は脳幹と大脳辺縁系および皮質の、それぞれの活動の相互作用であり、さまざまな脳活動が注意の強さに依存する。一般にわれわれは、騒音の中にいても、ある特定の音や声を聞き分けることが可能である(カクテルパーティー現象)。両側耳に呈示した複数の異なる周波数の純音のうち、特定の音に選択的に注意を向けた場合、その音に対する応答磁場が有意に増加することが明らかにされている(図7、p15)[6]。

言 語

多くの言語機能に関する研究において、視聴覚的に呈示された語の了解や語の作成にかかわる脳活動の時間的流れも(一次視聴覚野から側頭部、下頭頂部、後下前頭部そして運動野)、全頭型MEGの出現により明らかになった[7]。また、母音刺激では左半球での応答が有意であることから、言語優位半球ならびに言語領域の同定が試みられている[8, 9]。

単語を読む際には、視覚的に入力された単語を特定するために、単語の形や音に関する知識(語彙表象)が検索され、感覚情報との照合が行われる(語彙アクセス)。単語認知に関する心理学的なモデルでは、その際、入力された単語の語彙表象だけではなく(例:こんや→コンヤ)、それと類似した単語の語彙表象も候補として検索され(候補の生成、例:こんや→コンキ、コンド、ホンヤなど)、そのなかから適切なものが選ばれると仮定されている。この類似語の候補の生成と抽出は、左上側頭部において処理されており、特に類似語数の多い単語が刺激呈示された場合で、より強度に脳活動が賦活される(図8、p15)[10]。

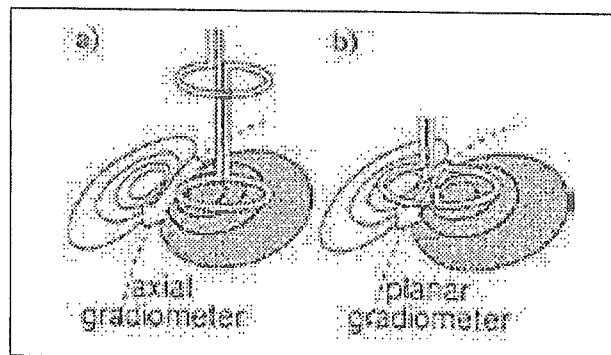失読症(dyslexia)では、単語呈示後約100ミリ秒での後頭内側部の活動には健常者との変化を認めず、文脈の中での単語の意味付けにおいて、文脈中の語彙理解に関係すると考えられる左上側頭部の活動が、健常者より約100ミリ

図1 電流源と磁場分布
頭表に水平な電流源の直上の頭皮上に、双極状に磁場分布が形成されている。この磁場分布に基づいて、脳内活動源が推定される
灰色部分:磁場の吹き出し、白色部分:磁場の吸い込み。小矢印:脳溝内に発生した電流源、大矢印:等価電流双極子

図2 MEGに用いられている磁場検出センサーの形状
a):一次微分軸型(axial型)。磁場の吹き出し、吸い込みを検出し、比較的深部の記録に適している
b):一次微分型(planar型)。センサー直下の活動を主として検出し、脳表の記録に適している

秒遅れ、応答磁場も有意に小さくなっていたなど、約150〜200ミリ秒の間で障害があることが明らかにされている[11]。これは、言語処理の前段階での障害によると考えられ、健常者と失読症患者では、文脈全体の中で単語を認識処理する過程が異なることを示唆している。

単語の発話は、健常者では刺激呈示後400ミリ秒以内に左下前頭部・左運動野・運動前野の順に活動するのに対して、吃音者ではこの順序が逆になっているという[12]。これは発音のコード化の前に、運動準備が始まっている可能性を示唆

するものである。また、発話中には健常者では右運動野・運動前野の活動も認められるが、吃音者では認められなかったという[12]。

感覚運動連関機形

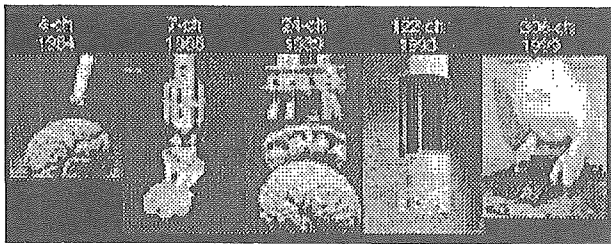手指の動きや口唇形状のみを変化させた顔の静止画像の観察、模倣、ならびに自動動作に同期した脳活動について明らかにされている[13, 14]。手指の動作の観察にかかわる脳活
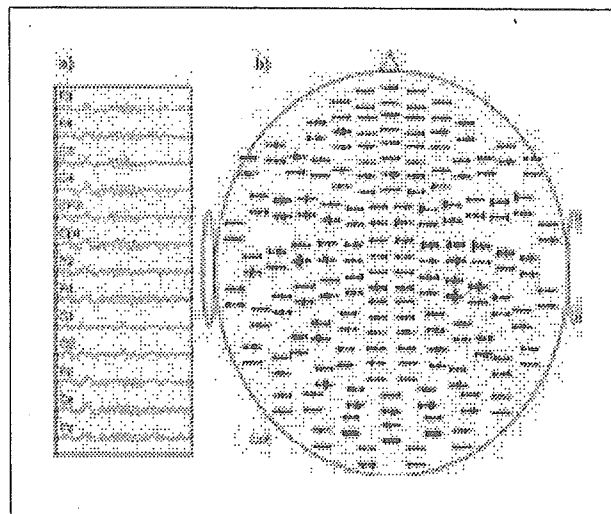

図3　MEGの進化
少数チャンネルから、全頭を覆う多チャンネルへと開発が進められた

図4　頭皮上脳波と脳磁場の同時記録による睡眠紡錘波
a)：頭皮上脳波記録より、紡錘波を認める主要チャンネルを抜粋。中心頭頂部を中心に14Hzの紡錘波を認める
b)：脳波と同潜時帯におけるMEGによる紡錘波形（204チャンネル分を表示）。左右両半球で、中央部チャンネルを中心に広汎に分布しているのがわかる
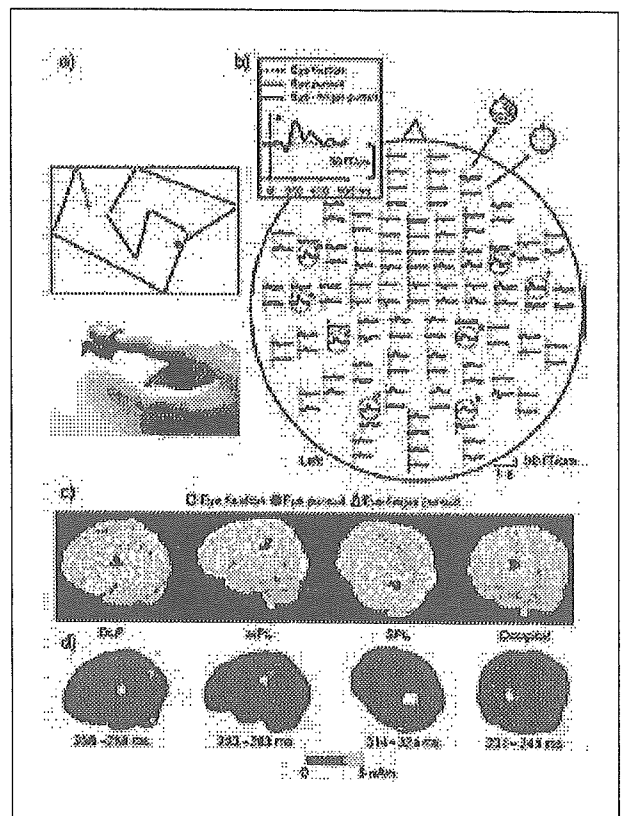
図5　視覚性滑動性追跡運動時における脳活動
a)：被験者の眼前に設置されたスクリーン上のフレーム内を滑動性に移動し、かつフレームの辺縁で反射する標的を、両側眼球、両側眼球および右手第2指にて追跡する
b)：MEGによる応答磁場波形
c)：MRI上に重畳した、両側半球の後頭部・前下頭頂部・外側前頭部・上頭頂部に推定された主活動源
d)：脳表の磁場分布による活動源を表す。後頭部、前下頭頂部、外側前頭部、そして上頭頂部の順に活動が推移していた。それぞれの部位における活動は、眼球と手指による追跡・模倣課題遂行時に、またいずれの課題においても、前下頭頂部が最大に活動していた
DLF：dorsolateral frontal area、aIPL：anterior inferior parietal lobule、SPL：superior parietal lobule、Occipital：occipital area　　　　　　　（Nishitani et al. 1999[4]より改変）
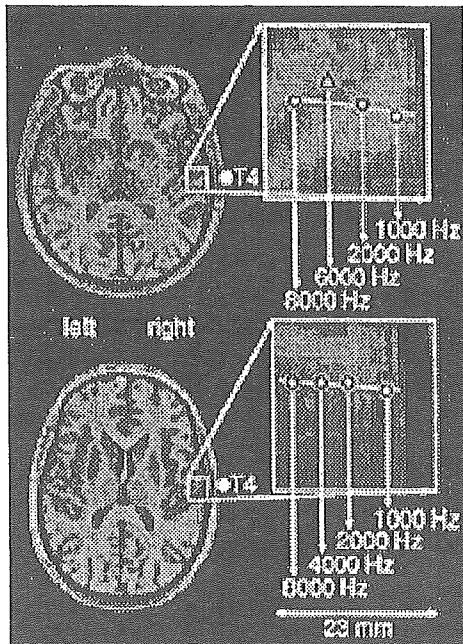
図6 一次聴覚野の各周波数に対応した応答部位
耳鳴りの周波数による音刺激に対する一次聴覚野の応答部位が、耳鳴り患者（上段）において、その空間配列が逸脱していることが、健常者（下段）と比較してわかる　　　　（Muhlnickel et al. 1998 [5]より引用）
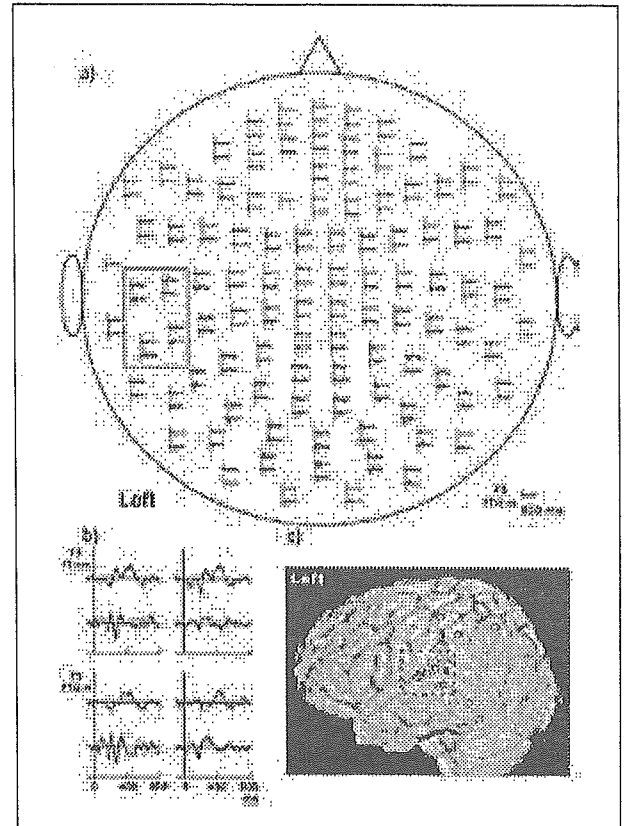

図8 類似語に関連する脳活動
この結果は、類似語の語彙表象へのアクセスが、特に候補語数の多い単語においてより多く、その処理が左上側頭部において行われていることを示唆するものであると考えられる
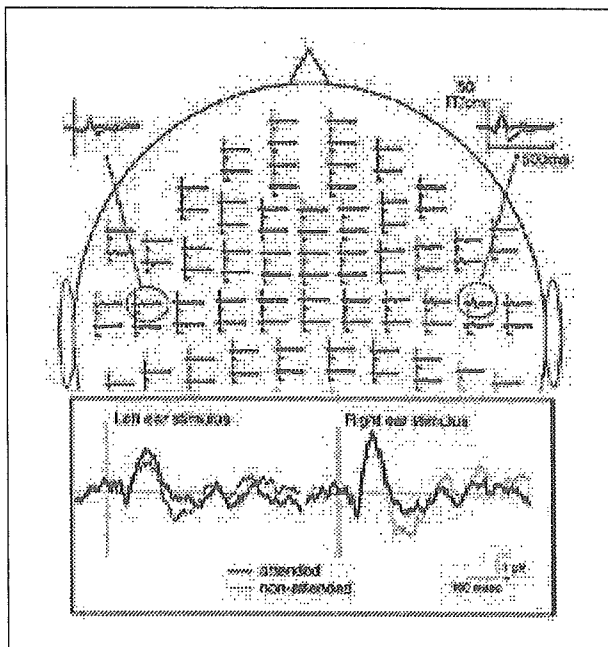（Sekiguchi et al. 2003 [10]より改変）

図7 聴覚誘発脳磁場と選択的注意の影響
上段：左耳に呈示された頻回トーンバーストに対する注意関連磁場応答波形。注意関連磁場応答は、両側半球側頭部に認める。赤線および青線：注意および非注意時の応答磁場波形
下段：左右耳それぞれに呈示された頻回トーンバーストに対する頭皮上電極Fzにおける事象関連電位。太線および細線：注意および非注意状態での反応　　　（Fujiwara et al. 1998 [6]より改変）
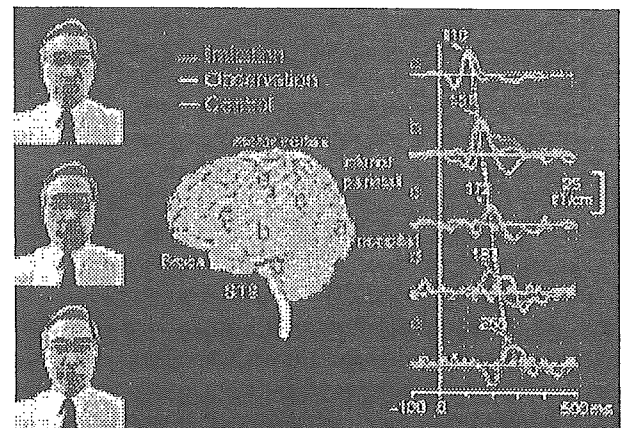

図9 口唇形状の観察・模倣における脳磁場応答波形と主要活動部位（左半球）
大脳皮質内では、後頭部、上側頭溝、下頭頂部、後下前頭部（ブローカ野）、一次運動野の順に活動することが明らかになった。言語性口唇形状の同様の課題、また右半球においても同様の活動を認めた。模倣において、後下前頭部（ブローカ野）、一次運動野で活動が有意に大きくなることを認めている　　　（Nishitani and Hari, 2002 [14]より改変）

動は、最初に後頭部が、次にブローカ野（特にブロードマン44野）、左側運動野、そして右側運動野の順に活動を認めた。また口唇形状のみを変化させた顔の静止画像の観察、模倣課題時での活動は、後頭部視覚野、上側頭溝、下頭頂部、ブローカ野、そして一次運動野の順に認められた。いずれの場合も、ブローカ野と一次運動野の活動の大きさは、模倣課題時で最大であった。左半球の活動は、言語化可能な口唇形状に対する課題のほうが言語化不可能な口唇形状に対するより優位であり、右半球ではその逆であった（図9、p15）。

さらに、模倣困難を呈するAsperger syndromeの患者における口唇形状の模倣時の脳活動を、健常者の結果と比較した[15]。それによると、両側半球のブローカ野と運動野の活動は有意に小さく、かつ応答潜時が遅延していた。この結果は、Asperger syndromeの模倣障害、新しいスキルの獲得における障害の機序を考えるうえで貴重なデータと考えられる。

他人の動作、もしくは動作を示唆する静止画像・写真を観察している場合でも、自ら同様の動作を遂行したときのように、これらの領域が活動することを示しており、他人の動作をあたかも自らの動作として映し出しているかのようなことから、Human Mirror Neuron System（HMNS）とよんだ[13, 16, 17]。以上の研究は、後下前頭部（BA 44）は動作の理解とその再現に重要な役割を担っていることを示唆するものである。

MEGは完全な非侵襲的記録法で反復記録が可能であること、優れた時間・空間分解能を保有していること、MEG計測装置の多チャンネル化が実現したことなどから、臨床検査法のひとつとして確立されつつある。今後、fMRIなどの他の脳機能評価方法との有機的連携により、脳機能に関連する研究と臨床応用に貢献するものと期待されている。📖

文　献
1) De Renzi E, Prosopagnosia. In: Feingerg TE, Farah MJ, editors. Behavioral Neurology and Neuropsychology. NewYork: Mac-Graw-Hill; 1997. p. 245-55.
2) Halgren E, Raij T, Marinkovic K, Jousmaki V, Hari R. Cognitive response profile of the human fusiform face area as determined by MEG. Cereb Cortex 2000; 10 (1): 69-81.
3) Perenin M-T. Optic ataxia and unilateral neglect. In: Their P, Karnath H-O, editors. Clinical evidence for dissociable spatial functions in posterior parietal cortex. Parietal lobe contributions to orientation in 3D space. Berlin: Springer-Verlag; 1997. p.289-308.
4) Nishitani N, Uutela K, Shibasaki H, Hari R. Cortical visuomotor integration during eye pursuit and eye-finger pursuit. J Neurosci 1999; 19 (7): 2647-57.
5) Muhlnickel W, Elbert T, Taub E, Flor H. Reorganization of auditory cortex in tinnitus. Proc Natl Acad Sci USA 1998; 95 (17): 10340-3.
6) Fujiwara N, Nagamine T, Imai M, Tanaka T, Shibasaki H. Role of the primary auditory cortex in auditory selective attention studied by whole-head neuromagnetometer. Brain Res Cogn Brain Res 1998; 7 (2): 99-109.
7) Dhond RP, Buckner RL, Dale AM, Marinkovic K, Halgren E. Spatiotemporal maps of brain activity underlying word generation and their modification during repetition priming. J Neurosci 2001; 21 (10): 3564-71.
8) Simos PG, Breier JI, Zouridakis G, Papanicolaou AC. Assessment of functional cerebral laterality for language using magnetoencephalography. J Clin Neurophysiol 1998; 15 (4): 364-72.
9) Papanicolaou AC, Simos PG, Breier JI, Zouridakis G, Willmore LJ, Wheless JW, et al. Magnetoencephalographic mapping of the language-specific cortex. J Neurosurg 1999; 90 (1): 85-93.
10) Sekiguchi T, Nishitani N, Nakajima Y. Effect of neighborhood size on cortical magnetic responses during word completion task. Neurosci Res 2003; 46 (Suppl 1): S168.
11) Helenius P, Salmelin R, Service E, Connolly JF. Semantic cortical activation in dyslexic readers. J Cogn Neurosci 1999; 11 (5): 535-50.
12) Salmelin R, Schenitzler A, Schmitz F, Freund HJ. Single word reading in developmental stutterers and fluent speakers. Brain 2000; 123 (6): 1184-202.
13) Nishitani N, Hari R. Temporal dynamics of cortical representation for action. Proc Natl Acad Sci USA 2000; 97 (2): 913-8.
14) Nishitani N, Hari R. Viewing lip forms: Cortical dynamics. Neuron 2002; 36 (6): 1211-20.
15) Nishitani N, Avikainen S, Hari R. Abnormal imitation-related cortical activation sequences in Asperger's syndrome. Ann Neurol 2004; 55 (4): 558-62.
16) Hari R, Nishitani N. From viewing of movements to understanding and imitation pf other person's acts: MEG studies of the human mirror-neuron system. In: Kanwisher N, Duncan J, editors. Functional neuroimaging of visual cognition: Attention and Performance XX. New York: Oxford Univ. Press; 2004. p.463-79.
17) Nishitani N, Schürman M, Amunts K, Hari R. Broca's region: From action to language. Physiology 2005; 20 (2): 54-63.

MEG

MEG (Magnetoencephalography)

室長

西谷　信之

Nobuyuki NISHITANI

国立身体障害者リハビリテーションセンター研究所感覚機能系障害研究部感覚認知障害研究室

KEY WORDS

脳磁場計測
MEG
脳磁図
脳機能評価
臨床応用

SUMMARY

優れた時間並びに空間分解能を有し，頭部の構造物による信号の歪みがない脳磁場計測法は，基礎的な脳機能解明に加えて，腫瘍性疾患やてんかんなどの術前評価のみならず，他の脳疾患においても非侵襲的臨床検査法としてしだいに応用されつつある。

はじめに

脳磁場計測 (magnetoencephalography：MEG) による頭蓋外からの微弱脳磁場の計測が行われたのは，脳波の出現後40年を経た1960年代後半のことであった．その後1970年代に超伝導量子干渉素子装置が開発され，脳磁場計測がより現実的なものとなった．その結果，電気的な基準を必要とせずにヒト脳の随意脳活動や誘発磁場信号の記録が可能となった．更に近年の科学技術の急速な進歩により，記録センサーの増加と解析法が進化し，脳機能解明研究とともに臨床応用が進められている．

脳磁場の発生機序

脳機能の解明においては，脳活動の時間的関係を明らかにすることが重要である．MEGは，ミリ秒 (msec) レベルの時間分解能を保有し，脳機能のダイナミクスを解明することが可能な非侵襲的手法である．

ヒトの脳より発生する磁場は地球の定常磁場の約1億分の1に相当する非常に弱い信号であるため，頭皮上で計測されるためには，神経配列に規則性を持った神経細胞の一群が同期して発火する必要がある．大脳皮質運動野第V層に存在する錐体細胞は，細胞体から皮質表層に向かって樹状突起が分布している．MEGが計測する脳磁場は，主としてこの大脳皮質錐体細胞への興奮性シナプス後電位 (excitatory post-synaptic potential：EPSP) により生じる細胞内電流によるものである．

現在ほとんどのMEGでは，頭皮と平行に計測コイルが設置され，そのコイルを貫く磁場をもとに，頭皮上の磁場分布並びに脳活動を評価している．脳溝に位置し，脳表に平行な尖樹状突起内の細胞内電流が形成する垂直方向の磁場成分をMEGは記録するのに対して，EEGは脳表に対して垂直水平両

方向の細胞外容積電流を計測すること
から，両者は相補的な関係にある．

EEGに勝るMEGの最大の利点は，
電位分布には影響を与える，頭蓋の構
造物による磁場信号の歪みを認めない
点である．頭蓋骨，脳脊髄液，脳，硬
膜などの頭部の構成組織の透磁率は均
一と見なされるため，頭部術後や頭部
挫傷後などの構成組織の変化による頭
皮上の磁場信号とその分布には歪みが
生じない．その結果，MEGは密度の
高い細胞内電流を計測することとあわ
せて，脳内活動源を数mm以内の誤差
で推定することができる．また，EEG
は基準電極に対する相対的な量を測定
するのに対して，MEGは絶対量であ
る磁束密度を計測しているため，基準
を必要としない．一方MEGの欠点は，
表面的な活動源を良好に限局できるが，
磁場強度が距離の2乗ないし3乗に反
比例して急速に減衰するために，深部
活動減の限局を苦手とする．

| MEGによる脳機能評価

MEGにより様々な脳機能の解明研
究が精力的に進められ，多くの知見が
得られている（表1）．

1．背景自発脳活動

背景自発脳活動に認められる周波数
がそれぞれ種々の脳活動を反映してい
ることは知られているが，MEGによ
る脳機能評価としての特徴は，機能局
在と同時に脳活動のリズムを明らかに
できることである．例えば，運動皮質
に認められる20Hzや40Hz帯域のリズ
ムと筋放電との相関は，随意運動の運
動野支配の機序や運動神経疾患の病態
生理を理解する上で重要である．睡眠
時第2段階に認められる紡錘波の頭皮

表1　脳磁場計測による脳機能評価
自発脳磁場活動
　睡眠時脳磁場活動
　発作性脳磁場活動
誘発脳磁場活動
　一次体性感覚，聴覚，視覚誘発磁場活動
高次脳磁場活動
　注意，記憶，認知，言語，計算，学習
運動関連脳磁場活動
感覚運動連関脳磁場活動

上分布と周波数に基づく発生機序の解
明にも，MEGは応用されている．

2．体性感覚誘発磁場（somatosensory evoked magnetic field：SEF）

末梢神経電気・触覚刺激により，刺
激後20～30msecで早期SEF（N20m）が，
35～70msecで後期SEF（N40m，P60m）
が誘発され，刺激対側半球の中心後回
に存在する一次体性感覚野（SI）の3b
野と1野に，それぞれ主活動源が推定
されている[1]．シルビウス裂とローラ
ンド溝交差部後方の二次体性感覚野
（SII）は，両側からの感覚入力を受け
る[2]．痛覚刺激によるSEFは1野由来
とされている[3]．痛覚刺激では，刺激
対側のSIとSIIおける反応開始が刺
激後約130msec前後でほとんど同時で
あることから，視床から平行してSI
とSIIに投射すると考えられる．

3．視覚誘発磁場（visual evoked magnetic field：VEF）

パターン反転全視野刺激により，
N75m，P100m，N145mの発生源が後
頭葉鳥距溝外側部付近に，また片眼の
フラッシュ刺激では健常者で両側後頭
葉に活動源が推定されている[4]．上4
分の1視野刺激より下4分の1視野刺
激の方が，50～70msec後に出現する
後頭葉鳥距溝の活動は大きく，半視野
刺激によるVEFは下4分の1視野刺激

によるそれに類似していることから，
複雑な視覚情報処理過程は下視野が優
勢である[5]．動きに対しては両側後外
側側頭部（MT/V5）に活動源が推定さ
れている[6]．

4．聴覚誘発磁場（auditory evoked magnetic field：AEF）

刺激後約50msecで中潜時AEF
（P50m）が対側優位に出現し，100msec
で誘発されるAEF（N100m/N1m）は，
刺激同側におけるAEFよりも対側のそ
れの方が短潜時（約10msec），高磁場で，
その電流源はともに両側上側頭回
（Heschl回）に推定されている．また，
純音刺激に対するAEFは左半球に比べ
て右半球の方が短潜時，高磁場である．
空間的に配置された音源からの音刺激
に対するAEFは右半球一次聴覚野の優
位性が示されている[7]．刺激音の周波
数とN100mの推定発生源の位置との関
係では，周波数が高くなるに従って推
定電流源は深くなる（spatial tonotopy）．

5．注意（attention）

我々は騒音のなかにいても，ある特
定の音や声を聞き分けることが可能で
ある（カクテルパーティー現象）．左右
いずれの耳へ選択的に注意を向けても，
一次聴覚応答N100mの応答潜時には変
化が認められないが，それぞれの振幅
及び推定される活動源の大きさが有意
に増大する[8]．この結果は特定の音に
対して選択的に注意を向けることで，
一次聴覚野の活動が亢進したために生
じた現象であることを示している．

6．言語（language）

視聴覚提示された語の了解や語の作
成にかかわる脳活動の時間的流れも
（一次視聴覚野から側頭部，下頭頂部，

後下前頭部そして運動野), 全頭型MEGの出現により明らかになった[9][10]. 失読症患者では, 後頭内側部の活動(単語呈示後約100msec)は健常者と変化が見られなかったが, 文脈での単語の意味づけの段階(約150～200msec)で障害されていた[11]. 文脈全体で単語を認識処理する過程が健常者と失読症患者では異なることを示唆している. 更に, 中・後側頭部, 下頭頂部そして後下前頭部における呼称, 音韻処理, 単語想起などに関連する詳細な言語機能の知見が得られている[12][13]. 単語の音読では, 類似語数の多い単語が刺激提示された場合で, より強度に脳活動が賦活された[14]. 母音刺激では左半球での応答が有意であることから, 特に単語認識課題でのMEGの応答並びにその活動源推定結果とWadaテスト[15]との比較を行い, MEGは言語優位半球の非侵襲的同定に有用であるとの報告もなされている[16][17]. 左半球における言語特異領域が, 動静脈奇形や部分切除術後に右半球の相当部位や左半球の後部に移動していたとする報告もあり, 言語領域の可塑性を示唆している[18].

7. 認知(cognition)

一般に深部領域からの磁場信号の記録は困難とされている. 内側側頭部に位置する海馬や扁桃体もその1つである. しかし, てんかん源性発作波に比べて後期誘発成分は頭皮上に波及しやすく, 誘発波形の加算によりS/N比を向上させることで磁場信号の記録は可能となる. 聴覚オッドボール課題で, 認知機能を反映すると考えられているP300に相当する応答磁場波形の発生源が, 健常者や難治性てんかん患者の選択的切除術前後の記録から, 両側半球の側頭葉内側部(海馬), 上側頭部と下頭頂部に推定されている[19][20]. 顔の認知に関しては, 機能画像などにおいても研究が進んでおり, 特に右紡錘状回が特異的に活動すると報告されている. MEGでの研究では, 顔刺激後約120msecで右紡錘状回を含む後下側頭部が活動するとされている[21].

8. 運動関連脳磁場(movement-related cortical magnetic field : MRCF)

随意運動に伴って頭皮上から記録される運動関連脳電位に相当する脳磁場活動として, 運動関連脳磁場(movement-related cortical field : MRCF)が知られている[22]. 手指などの随意運動時には, 運動開始約1～1.5秒前より運動対側優位に, EEGでのbereitschaftspotential (BP)に相当する磁場(readiness field : RF)が記録され, RF終点近傍の磁場はmotor field (MF)とされている. RFの運動開始前200～900msecで中前頭葉(Brodmann 9野)に, またそれに引き続いて補足運動野, 前運動野, 一次運動野(the primary motor cortex : M1)の順に電流源が推定されている[23]. 運動後の活動として, movement evoked field I & II (MEF I & II)があり, MFとMEF Iの電流源はそれぞれ中心溝前壁, 後壁に推定され, 運動野と感覚野の関連が示唆されている[24]. MFは皮質脊髄路の活動に密接に関連し, post-MFは求心性感覚入力による皮質活動を表していると考えられる. 更に運動同側のMFが感覚入力によって干渉されることから, 運動野と感覚野の相互作用が両半球において平行して生じていることが示唆される[25]. 運動時のM1の活動は, 運動対側のみならず同側M1においても認められ, その活動の大きさは対側優位である[26]. M1における手指の領域と利き手の関係では, 利き手対側の"優位" M1における手指の占める領域が同側よりも広いことが知られている[27].

9. 感覚運動連関脳磁場活動

普段我々は, 視聴覚・触覚などの一次感覚情報を受容野より受け入れ, 脳内での情報処理を経て, 感覚入力に応じた応答を一次運動野の活動として運動器官を通して表現している.

眼球と手指による標的の滑動性追跡眼球運動時には, 両側半球で後頭部, 前下頭頂部, 外側前頭部, そして上頭頂部の順に活動する. 前下頭頂部が最大に活動しており, 連続する滑動性追跡運動の制御には, 前下頭頂部が重要であることが示唆された[28]. 手指の動きや口唇形状のみを変化させた顔の静止画像の観察, 模倣, 並びに自動動作に同期した脳活動について明らかにされている[29][30]. 手指の動作の観察にかかわる脳活動は, 最初に後頭部が, 次に前頭葉後下部:ブローカ野(特にBrodmann 44野), 左側運動野, そして右側運動野の順に活動を認めた. また口唇形状のみを変化させた顔の静止画像の観察, 模倣課題時での活動は, 両側半球の後頭部視覚野, 上側頭溝, 下頭頂部, ブローカ野, そして一次運動野の順に認められた. いずれの場合も, ブローカ野と一次運動野の活動の大きさは模倣時で最大であった. 左半球の活動は, 言語化可能な口唇形状の写真提示の方が言語化不可能なそれに対するより優位であり, 右半球ではその逆であった. 他人の動作もしくは動作を示唆する静止画像・写真を観察している場合でも, 自ら同様の動作を遂行した時のように, これらの領域が活動することを示しており, 他人の動作