

University of Groningen

Brains in interaction

Schippers, Marleen Bernadette

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2011

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Schippers, M. B. (2011). *Brains in interaction*. s.n.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

BROCA'S AREA: LINKING PERCEPTION AND PRODUCTION IN LANGUAGE AND ACTIONS

Published as: Rossi, E.¹, Schippers, M.B.¹, & Keysers, C. (2011). Broca's area: linking perception and production in language and actions. In Han, S., editor, *Culture and Neural Frames of Cognition and Communication, On Thinking*. Vol. 3. Springer Berlin Heidelberg

ABSTRACT

A distinction between action perception and production has always been emphasized by traditional accounts of brain function. The goal of this review is to show that this simple distinction seems no longer valid. Broca's area in particular seems to be important for both perception and production of language and action. Functional imaging studies suggest that Broca's area is active both when people produce and perceive syntactically complex sentences and while they produce and perceive complex actions. Lesions in this area disrupt the capacity to produce syntactically correct sentences and to perceive sentences in which syntax is essential. From an action-perspective, lesions to Broca's area disrupt the capacity to produce goal directed actions and to perceive the actions of others. Furthermore, the property and location of mirror neurons in the monkey might provide the reason why Broca's area in humans has a dual function in production and perception.

.....

2.1 INTRODUCTION

Traditional accounts of brain function have often emphasized a distinction between action perception and production. For instance, the occipital and temporal lobe were considered to deal with visual and auditory perception while the frontal lobe was considered to deal with the production of goal directed actions. In the domain of language as well, the classic distinction between Wernicke and Broca's aphasia suggested that one part of the brain deals with perceiving what other people say while the other deals with producing speech.

¹ Authors contributed equally to this bookchapter

The goal of this review is to show that this simple distinction seems no longer valid. In particular, we will show how both in the domain of language and action, a brain area, called Broca's Area, seems to be important for both perception and production. Finally, we will show how mirror neurons help us understand why and how a certain brain area can be important in both perception and production.

We will start by explaining where Broca's area is located in the brain. We will then show how lesions in this area disrupt the capacity to produce syntactically correct sentences and to perceive sentences in which syntax is essential. We will then show that lesions to Broca's area disrupt the capacity to produce goal directed actions and to perceive the actions of others. We will then review data from functional imaging studies that suggest that Broca's area is active both when people produce and perceive syntactically complex sentences and while they produce and perceive complex actions. Finally, we will review the property and location of mirror neurons in the monkey and suggest that they may be the reason why Broca's area in humans has a dual function in production and perception.

2.2 BROCA'S ANATOMY

The name 'Broca's area' comes from the French neurologist Pierre Paul Broca, who brought the inferior frontal gyrus into the spotlight as a possible location for the seat of language in the human brain. When he investigated the brains of his deceased patients who suffered from a "loss of speech", he found lesions located in the frontal lobe. He decided, however, not to dissect the brains and only described the lesions from the outside. He sent the brains to a museum in Paris giving neuroscientists nowadays the opportunity to use modern imaging techniques to investigate his original findings ([Cabanis et al., 1994](#); [Dronkers et al., 2007](#); [Castaigne et al., 1980](#)) From these images we know now that the lesions are not confined to parts of the inferior frontal gyrus only, but they extend medially into the arcuate/superior longitudinal fasciculus, which connects anterior and posterior language regions ([Geschwind, 1972](#)).

The original finding of Broca, however, has led to a substantial amount of research on Broca's area and these studies have made it further clear that Broca's area does not consist of one cytoarchitectonically well-defined area, but comprises several areas, including Brodmann areas (BA) 44 and 45 and the ventral part of Brodmann area 6. In the remainder of this chapter, we will use the term Broca's area to indicate BA 44 and 45 and the ventral part of BA 6.

2.3 LESION STUDIES OF LANGUAGE

2.3.1 *Language production*

As introduced, the term ‘Broca’s aphasia’ has been minted after Paul Broca’s description of patient ‘Tan’ to address production language impairment due to a damage in the posterior half of the left inferior frontal gyrus. The label ‘Broca’s aphasia’, though, seemed very soon too broad and unspecific to describe the complex pattern of linguistic deficits related to a brain damage in the ‘language production areas’. After the fundamental studies of Arnold Pick (Pick, 1898, 1913) the term ‘agrammatism’ has been used to denote a type of Broca’s aphasia, which involves a specific impairment at the grammatical level. Since then, the production deficits seen in Broca’s aphasia and agrammatism have been described in a great number of lesion studies across languages (see Bates et al., 1991, for a review), studies which all converge in showing that lesions in Broca’s area result in a production deficit with a particular involvement of grammar. The production deficits observed in Broca’s aphasia are generally charac-

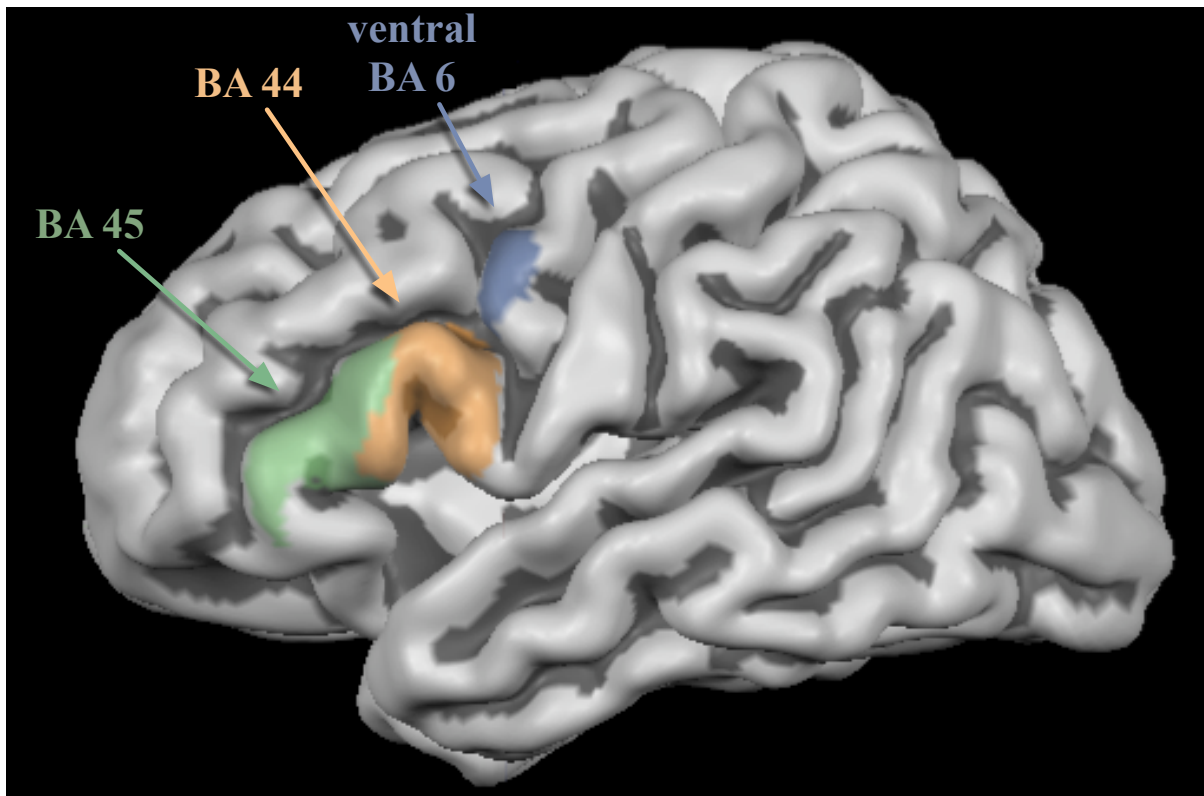


Figure 2.1: Broca’s area shown on the cortical surface of the brain. Broca’s area comprises several areas, including Brodmann areas (BA) 44 and 45 and the ventral part of Brodmann area 6.

terized by a decrease in speech rate, omission and/or substitution of function words (articles, prepositions, pronouns), a frequent use of uninflected verbs (particularly detectable in morphologically rich languages in which the non-finite form of verbs is morphologically marked, like Italian 'mangiare' - to eat), and a reduced use in the use of coordinated and subordinated sentences together with a loss of comprehension of complex syntactic structures. [Miceli et al. \(1984\)](#) showed that Italian aphasic speakers with a lesion in Broca's area omit free morphemes (articles and prepositions) and substitute bound morphemes (verb inflections for Tense and Person agreement). The same deficits were observed for German by [DeBleser et al. \(1996\)](#) and [Luzzatti and Bleser \(1996\)](#) who showed that agrammatic aphasic speakers were impaired in 'syntax-dependent morphology', i.e. morphological processes which are more directly linked to syntactic operations (like verbal inflection).

As far as language production goes, the data provided by lesion studies seem to converge in showing that lesions in Broca's area produce an agrammatic speech output, which suggests that these brain areas are the locus in which syntax is stored. But if Broca's area indeed represents the anatomical locus for syntax, once a damage is located in that area, a language impairment at the syntactic level should not only be detectable in production but also in comprehension.

2.3.2 *Language comprehension*

Thanks to a series of pioneer lesion studies on agrammatism ([Caramazza and Zurif, 1976](#); [Grodzinsky, 2000](#); [Luzzatti et al., 2001](#); [Shapiro and Levine, 1990](#)), it became clear that people with lesions in Broca's area (which had been addressed for a long time as the specific locus for language production) not only show deficits in production but they also show similar impairments in the comprehension of complex grammatical structures. [Caramazza and Zurif \(1976\)](#) were among the first to describe that patients with a lesion in Broca's area show deficits in comprehension of complex syntactic structures. The authors showed that agrammatic patients performed at chance when interpreting semantically reversible sentences, i.e. sentences that require a syntactic analysis to be correctly understood like: "The girl was kicked by the boy". In contrast, they performed above chance with sentences that could be interpreted using semantic rules as a disentangling strategy, such as: "The ball was kicked by the girl". Further studies on comprehension deficits in Broca's aphasia (e.g. [Grodzinsky, 1995](#); [Luzzatti et al., 2001](#)) report that other complex syntactic structures, like passive and subordinate sentences as well as sentences with pronominal clitic pronouns, are difficult to interpret for aphasic speakers.

Lesion studies have provided (and still provide) fundamental information on the role played by Broca's area in language processing, providing converging evidence that

Broca's area is involved both in language production and in language comprehension, disconfirming the initial thought that Broca's area was exclusively involved in language production. Second, the evidence is strong in favor of Broca's area being involved in syntactic processing, supporting the view that this area is the locus of grammatical encoding.

2.4 LESION STUDIES OF ACTIONS

Lesions in and around Broca's area are relatively well known for their association with Broca's aphasia, which we have discussed in the previous paragraphs. In this section, we will focus on how lesions in this part of the brain can cause disruptions in executing action and observing the actions of others.

2.4.1 *Action execution*

Deficits in producing actions are known as apraxia. Patients who suffer from apraxia have difficulties in executing learned movements even though they are physically able to perform these movements. The disorders aphasia and apraxia very often occur together (Renzi et al., 1980).

Lesions in Broca's area play an important role in apraxia (Leiguarda and Marsden, 2000). They can lead to weakness of muscles that control oro-facial, laryngeal and tongue movements (Förster, 1936). Furthermore, lesions in Broca's area can lead to difficulties in sequencing of actions (Harrington et al., 1998), to a loss of regularity of exploratory finger movements during manipulation of objects (Binkofski et al., 2001), to deficits in visuomotor associative learning (Binkofski and Buccino, 2004), and to deficits in grasping (Dettmers et al., 2003).

Natural lesions that are restricted to one cytoarchitectonically well-defined brain area are rare. Fortunately, with the technique of repetitive transcranial magnetic stimulation (rTMS), it is possible to create temporary 'lesions' in a particular brain area to investigate the necessity of this brain area during a certain task. To investigate the role of Broca's area during imitation of finger movements, Heiser et al. (2003) delivered rTMS over right and left Broca's area while participants had to perform this task. They found that these stimulations caused a disruption in the imitation task, while the control rTMS over the occipital cortex did not show such a disruption. This indicates that Broca's area could be the place in which a matching between observed and to-be-executed actions takes place. Since rTMS did not cause a disruption in a motor control task, the deficits in imitation could not have been caused by a disruption in planning or selection.

The design of this experiment was, however, criticized by Makuuchi (2005), who

argued that the movement that had to be imitated was too simple. This has as a consequence that only in the first few trials has the observed movement really to be transformed into one's own motor representation, but in later trials, the observed movement merely functions as a visual cue to perform a learned movement. [Makuuchi \(2005\)](#) performed a new experiment from which he concludes that it is not imitation that Broca's area is essential for, but it is the delayed execution of actions.

Damage to Broca's area thus does not only have an influence on the production and perception of language, but also disrupts action production.

2.4.2 *Action perception*

Besides disrupting action production, damage in Broca's area also has a profound influence on the perception of actions performed by other people. Damage to Broca's area leads to an impairment in conceptual knowledge about actions ([Tranel et al., 2003](#)).

Aphasic patients with lesions in the inferior frontal gyrus and the ventral premotor cortex have trouble with action understanding ([Saygin et al., 2004](#)). This is independent of whether the action is presented linguistically (i.e. a written description) or non-linguistically (i.e. visual presentation). Furthermore, the linguistic and non-linguistic deficits are correlated with each other in the mild and relatively fluent aphasics, which implies a common underlying cause of the deficits. Artificially lesioning this area with TMS disrupts action understanding of other people's actions ([Pobric and de C Hamilton, 2006](#)). These results are in accordance with results of [Aziz-Zadeh et al. \(2006\)](#), who (in non brain damaged subjects) found overlapping activations for action observation and reading sentences about actions in Broca's area.

[Pazzaglia et al. \(2008\)](#) provide evidence that indicate that the deficits in action production are related to deficits in action perception. First, they showed that brain-damaged patients who suffer from limb apraxia also show a greater impairment in recognition of gestures than brain-damaged patients who do not suffer from this disorder. Second, premotor and parietal lesions that impair hand action execution (as compared to mouth action execution) also selectively impair the recognition of hand gestures and their sounds ([Pazzaglia et al., 2008](#)).

All these studies show that deficits in action comprehension and action production are very much interrelated and associated with Broca's area.

2.5 FUNCTIONAL STUDIES ON LANGUAGE

If lesion studies inform us on the specific linguistic deficits that Broca's patients show in production and comprehension, the growing use in linguistic research of

neuroimaging techniques such as fMRI (functional Magnetic Resonance Imaging), ERP (Event-Related Potentials), MEG (Magnetoencephalography) and PET (Positron Emission Tomography) has made possible the investigation of language processing in healthy people. fMRI and PET, with their high spatial resolution permit the localization of particular brain areas which are involved during specific language tasks. PET is used more often for production studies given that it is less sensitive to movement and muscular artifacts, whereas fMRI has been extensively used in comprehension paradigms.

2.5.1 *Language production*

In a PET study [Indefrey et al. \(2001\)](#) elicited the production of sentences, which were increasingly grammatically complex. Participants were asked to describe short animated movies, which involved non-animated participants (a circle, an ellipse and a square). Results showed that the production of syntactically more complex sentences resulted in an activation of the left anterior operculum, caudally adjacent to BA44. [Haller et al. \(2005\)](#) performed an fMRI study involving open speech production. Participants were required to generate sentences given bare syntactic constituents (for example using the constituents: 'child', 'throw' and 'ball', participants should produce sentences like: 'The child throws the ball'). The activation resulting from the sentence generation task was compared with a sentence reading and a word repetition tasks. Both contrasts revealed that BA44/45 and BA6 were activated. Word level production studies involving syntactic processing have also been performed. [Jaeger et al. \(1996\)](#) and [Indefrey et al. \(1997\)](#) investigated which are the neurocorrelates of regular and irregular past verb formation. According to linguistic accounts, regular past verbs are formed using morpho/syntactic rules, for example in English, affixing the -ed morpheme to the verbal root. Irregular past verbs, however, cannot be 'blindly' formed applying a morpho/syntactic rule but their specific forms need to be stored in the lexicon. The two studies report that producing the past tense of regular verbs activates inferior frontal regions (regions that have been found to be active in morpho/syntactic processes), whereas producing the past tense of irregular verbs activates middle temporal regions (more involved with lexical processes).

2.5.2 *Language comprehension*

[Ben-Shachar et al. \(2003\)](#) performed an fMRI study to check which were the areas involved in a specific syntactic operation, i.e. syntactic movement. Participants had to listen to sentences and after this make a grammatical judgment about them. Results show that Broca's area was activated when sentences contained a moved element.

Broca's area (together with Wernicke's regions in both hemispheres) was activated in another fMRI study by [Ben-Shachar et al. \(2004\)](#). In this study, the task consisted of a comprehension test with two other types of grammatical structures involving syntactic movement, i.e. topicalization and embedded questions. These authors consider the activation of the left Broca's area crucial for syntactic processes. [Meyer et al. \(2000\)](#) found an activation of the left Broca's area during auditory presentation of grammatically correct and incorrect sentences. [Fiebach et al. \(2001\)](#) conducted a study aimed at detecting the areas involved in syntactic transformation or in the detection of syntactic anomalies. The results revealed that BA 44/45 were active in sentences with syntactic transformations, and BA 44/6 were active while detecting syntactic anomalies. Area BA 44 was activated in a study by [Dapretto and Bookheimer \(1999\)](#), when participants had to focus their attention towards more syntactic aspects of sentences compared to more semantic ones.

Summarizing the results from these studies, it is possible to speak about a network of regions within Broca's area, which support syntactic processing both for production and language comprehension. More specifically, the left inferior frontal gyrus with areas BA 44/45 are actively involved in more complex syntactic processing, while the frontal operculum seems to support the detection of whether a structure is grammatical or not.

2.6 FUNCTIONAL STUDIES ON ACTIONS

2.6.1 *Action execution*

Activation in Broca's area is found during the programming of object directed action execution, particularly when the action is a complex motor act which requires a high degree of sensorimotor control ([Binkofski and Buccino, 2004](#)). In our laboratory, activation in Broca's area is always found when comparing object- directed action execution against rest ([Gazzola et al., 2006](#); [Gazzola and Keysers, 2008](#); [Gazzola et al., 2007a,b](#)).

Further evidence for the fact that Broca's area is involved in the motor programming of actions comes from a study by [Haslinger et al. \(2002\)](#) in which participants have to perform increasingly complex finger movements. Results show that the more complex the sequence of movements is, the more Broca's area is involved. Other studies by [Schubotz & Cramon \(2003; 2001; 2002a; 2002b; 2002c\)](#) have shown similar results in that the ventral premotor cortex part of Broca's area is engaged when a sequential-based prediction of the action has to be made (for example, to predict the end state of a sequence of movements).

Examples of other kinds of motor acts that involve Broca's area are grasping actions

(Decety et al., 1994; Ehrsson et al., 2000; Grafton et al., 1996), manipulation of objects (Binkofski et al., 1999), finger movements (Krams et al., 1998; Seitz and Roland, 1992), and gesturing (Fridman et al., 2006).

Summarizing, parts of Broca's area seems to be involved in action execution, particularly when the action is complex (both in terms of movement and sequencing) and is object-directed.

2.6.2 *Action perception*

Studies using movies of simple hand actions show that Broca's area is consistently activated when observing these simple hand or mouth actions (Buccino et al., 2001; Gazzola and Keysers, 2008; Gazzola et al., 2007b,a; Grafton et al., 1996; Rizzolatti et al., 1996b). Broca's area is particularly involved when the action is goal-directed and includes an object, for example grasping a little cup, biting and chewing an apple (Buccino et al., 2001). Not only the visual perception of an action involves Broca's area, but the mere sound of actions also elicits a response in this area (Gazzola et al., 2006).

It is argued that, for Broca's area to respond to observed action, the action needs to be part of the motor repertoire of the observer. For example, Broca's area responds to the observation of mouth actions of humans (speech pronunciation) and monkeys (lip smacking), but not to mouth actions of a dog (barking) (Buccino et al., 2004). Gazzola et al. (2007a) extend this finding by showing that Broca's area is also involved in actions the kinematics of which we cannot match onto our own motor repertoire, but of which we do understand the goal (e.g., 'human' actions performed by an industrial robot).

The fact that Broca's area was historically linked to language processing, raised the question whether activation in this region is truly due to the processing of the action or to a form of inner verbalization of the action (Decety et al., 1997; Grèzes and Decety, 2001). There is now, however, relatively wide agreement about the fact that the idea of 'silent speech' cannot account for the activation in Broca's area. If activation in Broca's area would be due to inner speech, then one would expect that imitation with the left or right hand would activate this area similarly; however, Koski et al. (2003) found a difference in activation due to imitation with one hand or the other. Second, inner speech would predict that hearing and performing hand and mouth actions should cause similar patterns of activity in premotor regions. Gazzola et al. (2006) and Etzel et al. (2008), however, showed that hand and mouth actions determine different patterns of activity, which are, however, similar during execution and perception. In another study, rTMS was applied over left and right BA 44, causing a disruption in the imitation process (Heiser et al., 2003). Could it be a disturbance in the silent verbalization of the action that disrupted the imitation? The authors

note that this is a highly unlikely explanation, since pre-verbal little children cannot verbalize actions but can imitate them.

Summarizing these functional studies, we can say that Broca's area is highly important for the perception of other people's actions and for programming the execution of complex actions of hands and mouth, given that these are not too repetitive.

2.7 MIRROR NEURONS & THE PUTATIVE MIRROR NEURON SYSTEM

In the previous section, we have seen that Broca's area is involved in both perception and production of complex actions. Is it truly the same neural substrate that is responsible for these different tasks? In the monkey's brain there is evidence for the idea that production and perception depend on the same neurons, so-called mirror neurons.

Mirror neurons were first discovered in Italy (Gallese et al., 1996; Pellegrino et al., 1992; Rizzolatti et al., 1996a). Activity from single neurons in the macaque monkey's brain had been recorded when the monkey was performing an action (i.e. grasping a peanut, shelling a peanut). The researchers discovered that some neurons in this area not only showed activity during action execution, but also when the monkey observed the researcher grasping a peanut or shelling it. Later, the same laboratory would show that some mirror neurons also respond to the sound of a similar action (Keysers et al., 2003; Kohler et al., 2002). These neurons thus have the special property of firing not only when the monkey performs an action but also when a similar action is perceived. Mirror neurons therefore show a direct connection between perception and action. The areas in which mirror neurons have been recorded from in the monkey are the rostral part of inferior area 6 (area F5) (Pellegrino et al., 1992; Gallese et al., 1996; Keysers et al., 2003; Kohler et al., 2002) and the rostral part of the inferior parietal lobule (area 7b) (Fogassi et al., 2005).

Since the moment of discovery of mirror neurons, the question arose whether such neurons would be present in the human brain. Indeed, evidence for a mirror neuron system in humans has been derived from neuroimaging and transcranial magnetic stimulation studies, with the former showing that a network of areas is active both while people perform actions and while they view or hear other people's actions (Gazzola et al., 2006; Keysers and Gazzola, 2006; Rizzolatti and Craighero, 2004). In humans, this system seems to include the dorsal premotor, somatosensory, cerebellar and posterior temporal cortex in addition to BA 44 and 6 and the inferior parietal lobule (Gazzola and Keysers, 2008).

But is it also true for humans that it is the same population of neurons that respond both to the observation and execution of actions? We cannot say anything about

individual neurons, but on the level of individual voxels², we can affirm that this is the case. [Gazzola and Keysers \(2008\)](#) have shown that within individual subjects, they are truly the same voxels that respond both to the perception and production of complex actions. In addition, in a recent study, [Etzel et al. \(2008\)](#), using an analysis technique known as multivariate classification, could show that the perception and execution of actions not only both recruit Broca's area, but that they indeed determine similar patterns of activity in Broca's area, a finding most compatible with the presence of mirror neurons in the human Broca's area.

Mirror neurons show activation both in response to the execution of an action and to the observation of an action. In the human brain, we have seen that Broca's area is part of the putative mirror neuron system and has similar properties: it is active during perception and production of complex actions. Could it be that these two areas have a common evolutionary ancestor? Probably yes: there is a wide agreement that area F5 finds its homologue either in BA 44, 45 or 6. There is, however, less agreement about where exactly in these three areas it is ([Amunts et al., 1999](#); [von Bonin and Bailey, 1947, 1961](#); [Campbell, 1905](#); [Grèzes et al., 2003](#); [Grèzes and Decety, 2001](#); [Morin and Grèzes, 2008](#); [Passingham, 1993, 1981](#); [Petrides, 2006](#); [Petrides and Pandya, 1994](#); [Rizzolatti and Arbib, 1998](#)).

The discovery of mirror neurons has led to the idea that we understand, at least in part, the goal-directed actions of others such as grasping and manipulating objects by activating our own motor and somatosensory representations of similar actions ([Buccino et al., 2001, 2004](#); [Gallese and Goldman, 1998](#); [Gazzola et al., 2006, 2007a](#); [Hamzei et al., 2003](#); [Heiser et al., 2003](#); [Iacoboni et al., 2005](#); [Keysers and Gazzola, 2006](#); [Keysers et al., 2003](#); [Kilner et al., 2007](#); [Nishitani and Hari, 2000](#)).

2.8 BROCA'S AREA: BETWEEN LANGUAGE AND ACTION

In the previous paragraphs, we reported a series of studies (both lesion and functional) that show that BA 44/45 and BA 6 are critical brain areas underlying language production and comprehension as well as action execution and perception. Several studies addressed the question whether action and language share a common functional architecture in the brain.

Within the linguistic domain, one well-known phenomenon observed in Broca's aphasia is the noun-verb dissociation. Broca's aphasic speakers are reported to comprehend (and produce) nouns better than verbs ([Miceli et al., 1984](#); [Zingeser and Berndt, 1990](#); [Rossi and Bastiaanse, 2008](#)). This observation gave rise to a large number of studies investigating the causes of this dissociation. The first careful anatomical

² A voxel is a volume element that constitutes the building blocks of a 3D MR image of the brain. A voxel is analogous to a pixel in a 2D image

study in an agrammatic patient who showed a selective impairment in action naming was conducted by [Damasio and Tranel \(1993\)](#), who described that the patient presented a lesion in the left pre-motor frontal cortex. [Saygin et al. \(2004\)](#) reported an action comprehension study with 29 aphasic patients. Patients were tested with a comprehension task involving the process of actions presented visually (with a relevant drawing - pantomime) and linguistically (with a sentence). Results showed that patients were impaired in the comprehension of both modes of presentation. [Arévalo et al. \(2007\)](#) tested 21 aphasic speakers and a control group. Participants had to name, read or repeat single words, which were nouns or verbs. Behavioral results showed that both aphasics and non-brain-damaged speakers were less accurate in naming verbs, but a cross-item analysis revealed that the crucial factor that influenced the performance was 'manipulability', and this was true across category (both for verbs and for nouns).

These studies importantly confirm that people with damage in language areas (BA 44/45) show difficulties in the comprehension of both language and pantomime actions which indicates that similar brain areas are recruited for both tasks, bringing evidence for a convergence between the areas that are important for language and pantomime processing.

[Hamzei et al. \(2003\)](#) explicitly addressed the question of whether action recognition and language production share a common functional architecture. They performed an experiment in which they instructed participants to either recognize an action shown in a picture or to silently verbalize an action verb written on the screen. They found an overlap between activation of the language and the action task in the Broca's area on a group level. On a single subject level, however, no overlap was found and no consistent spatial pattern could be detected between the two activation peaks. This indicates that there seems to be no functional subdivision for language and action in Broca's area.

The observation that language and action share common neural substrates opens the question of whether this occurs as a coincidence or whether this is the base for advocating a closer relation between the two systems.

There exist a number of speculative ideas about this. The first one is represented by the 'Motor Theory of Speech Perception' ([Lieberman and Mattingly, 1985](#)) which states that we understand speech by perceiving the phonetic information as intended gestures of the sender, represented in the brain as motor commands. [Galantucci et al. \(2006\)](#) reviewed this theory and gathered evidence for the claims that perceiving speech is perceiving gestures and that the motor system is recruited for this. Another idea for why both action and language perception and production have overlapping brain substrates is the hypothesis of 'embodied semantics', which claims that language comprehension stems from the internal referring to the actions that are conveyed by the language. This theory is supported by studies showing that listening to action-

related sentences activates the motor-related areas in the brain (Aziz-Zadeh et al., 2006; Hauk and Pulvermüller, 2004; Tettamanti et al., 2005). The third idea argues that language evolution originated from hand gestures, which is the reason they are represented in the same region in the brain (Rizzolatti and Arbib, 1998).

Acknowledgements

Eleonora Rossi and Marleen Schippers wrote the manuscript jointly, with equal contribution. Christian Keysers contributed to the outline of the chapter and provided critical comments.

The work was supported by a VIDI grant of the Dutch science foundation (N.W.O.), a Marie Currie Excellence grant of the European commission to Christian Keysers, and a Marica De Vincenzi grant to Eleonora Rossi.

BIBLIOGRAPHY

- Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H. B., and Zilles, K. (1999). Broca's region revisited: cytoarchitecture and intersubject variability. *The Journal of comparative neurology*, 412(2):319–41.
- Arévalo, A., Perani, D., Cappa, S., Butler, A., and Bates, E. (2007). Action and object processing in aphasia: From nouns and verbs to the effect of manipulability. *Brain and Language*, 100(1):79–94.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., and Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current biology*, 16(18):1818–23.
- Bates, E., Wulfeck, B., and MacWhinney, B. (1991). Cross-linguistic research in aphasia: an overview. *Brain and Language*, 41(2):123–48.
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D., and Grodzinsky, Y. (2003). The neural reality of syntactic transformations: evidence from functional magnetic resonance imaging. *Psychological Science*, 14(5):433–40.
- Ben-Shachar, M., Palti, D., and Grodzinsky, Y. (2004). Neural correlates of syntactic movement: converging evidence from two fmri experiments. *Neuroimage*, 21(4):1320–36.
- Binkofski, F. and Buccino, G. (2004). Motor functions of the broca's region. *Brain and Language*, 89(2):362–369.
- Binkofski, F., Buccino, G., Stephan, K. E., Rizzolatti, G., Seitz, R. J., and Freund, H.-J. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research*, 128(1-2):210–213.
- Binkofski, F., Kunesch, E., Classen, J., Seitz, R. J., and Freund, H. J. (2001). Tactile apraxia: unimodal apractic disorder of tactile object exploration associated with parietal lobe lesions. *Brain*, 124(Pt 1):132–44.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., and Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatosopic manner: An fmri study. *The European Journal of Neuroscience*, 13:400–404.

- Buccino, G., Binkofski, F., and Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language*, 89(2):370–376.
- Cabanis, Iba-Zizen, M., Abelanet, R., Monod-Broca, P., and Signoret, J. L. (1994). “tantan” the first paul broca’s patient with “aphemia” (1861): Ct (1979), & mri (1994) of the brain. *4th refresher course of the ESNR: language and the aphasias*. Nancy: *European Society of Neuroradiology*, 4:9–22.
- Campbell, A. (1905). *Histological studies on the localisation of cerebral function*. Cambridge University Press.
- Caramazza, A. and Zurif, E. B. (1976). Dissociation of algorithmic and heuristic processes in language comprehension: evidence from aphasia. *Brain and Language*, 3(4):572–82.
- Castaigne, P., Lhermitte, F., Signoret, J. L., and Abelanet, R. (1980). Description and scanographic study of leborgne’s brain. broca’s discovery. *Revue neurologique*, 136(10):563–83.
- Damasio, A. R. and Tranel, D. (1993). Nouns and verbs are retrieved with differently distributed neural systems. *Proceedings of the National Academy of Sciences of the United States of America*, 90(11):4957–60.
- Dapretto, M. and Bookheimer, S. Y. (1999). Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron*, 24(2):427–32.
- DeBleser, R., Bayer, J., and Luzzatti, C. (1996). Linguistic theory and morphosyntactic impairments in german and italian aphasics. *Journal of Neurolinguistics*, 9(3):175–185.
- Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., and Fazio, F. (1997). Brain activity during observation of actions. influence of action content and subject’s strategy. *Brain*, 120 (Pt 10):1763–1777.
- Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J. C., and Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature*, 371(6498):600–2.
- Dettmers, C., Liepert, J., Hamzei, F., Binkofski, F., and Weiller, C. (2003). Läsion im ventrolateralen prämotorischen kortex beeinträchtigt die greiffunktion. *Aktuelle Neurologie*, 30:247–255.

- Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., and Cabanis, E. A. (2007). Paul broca's historic cases: high resolution mr imaging of the brains of leborgne and lelong. *Brain*, 130(Pt 5):1432–41.
- Ehrsson, H. H., Fagergren, A., Jonsson, T., Westling, G., Johansson, R. S., and Forssberg, H. (2000). Cortical activity in precision- versus power-grip tasks: an fmri study. *Journal of Neurophysiology*, 83(1):528–36.
- Etzel, J. A., Gazzola, V., and Keysers, C. (2008). Testing simulation theory with cross-modal multivariate classification of fmri data. *PLoS ONE*, 3(11):e3690.
- Fiebach, C. J., Schlesewsky, M., and Friederici, A. D. (2001). Syntactic working memory and the establishment of filler-gap dependencies: insights from erps and fmri. *Journal of Psycholinguistic Research*, 30(3):321–38.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., and Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science*, 308(5722):662–7.
- Förster, O. (1936). The motor cortex in man in the light of hughlings jackson's doctrines. *Brain*, 59:135–159.
- Fridman, E. A., Immisch, I., Hanakawa, T., Bohlhalter, S., Waldvogel, D., Kansaku, K., Wheaton, L., Wu, T., and Hallett, M. (2006). The role of the dorsal stream for gesture production. *Neuroimage*, 29(2):417–28.
- Galantucci, B., Fowler, C. A., and Turvey, M. T. (2006). The motor theory of speech perception reviewed. *Psychonomic Bulletin & Review*, 13(3):361–77.
- Gallese, V., Fadiga, L., Fogassi, L., and Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119(2):593–609.
- Gallese, V. and Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 12:493–501.
- Gazzola, V., Aziz-Zadeh, L., and Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current biology*, 16(18):1824–9.
- Gazzola, V. and Keysers, C. (2008). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: Single-subject analyses of unsmoothed fmri data. *Cerebral Cortex*, 19(6):1239–1255.
- Gazzola, V., Rizzolatti, G., Wicker, B., and Keysers, C. (2007a). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *Neuroimage*, 35:1674–1684.

- Gazzola, V., van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., and Keysers, C. (2007b). Aphasics born without hands mirror the goal of hand actions with their feet. *Current biology*, 17(14):1235–40.
- Geschwind, N. (1972). Language and the brain. *Sci Am*, 226(4):76–83.
- Grafton, S. T., Arbib, M. A., Fadiga, L., and Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. observation compared with imagination. *Experimental Brain Research*, 112(1):103–111.
- Grèzes, J., Armony, J., Rowe, J., and Passingham, R. E. (2003). Activations related to mirror and canonical neurones in the human brain: An fmri study. *Neuroimage*, 18:928–937.
- Grèzes, J. and Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Human Brain Mapping*, 12(1):1–19.
- Grodzinsky, Y. (1995). Trace deletion, theta-roles, and cognitive strategies. *Brain and Language*, 51(3):469–97.
- Grodzinsky, Y. (2000). The neurology of syntax: language use without broca's area. *Behavioral and Brain Sciences*, 23(1):1–21; discussion 21–71.
- Haller, S., Radue, E. W., Erb, M., Grodd, W., and Kircher, T. (2005). Overt sentence production in event-related fmri. *Neuropsychology*, 43(5):807–14.
- Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C., and Büchel, C. (2003). The human action recognition system and its relationship to broca's area: an fmri study. *Neuroimage*, 19(3):637–44.
- Harrington, D. L., Haaland, K. Y., and Knight, R. T. (1998). Cortical networks underlying mechanisms of time perception. *The Journal of Neuroscience*, 18(3):1085–95.
- Haslinger, B., Erhard, P., Weilke, F., Ceballos-Baumann, A. O., Bartenstein, P., von Einsiedel, H. G., Schwaiger, M., Conrad, B., and Boecker, H. (2002). The role of lateral premotor-cerebellar-parietal circuits in motor sequence control: a parametric fmri study. *Cognitive Brain Research*, 13(2):159–68.
- Hauk, O. and Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21:191–201.
- Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., and Mazziotta, J. C. (2003). The essential role of broca's area in imitation. *The European Journal of Neuroscience*, 17(5):1123–8.

- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., and Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, 3(3):e79.
- Indefrey, P., Brown, C., Hagoort, P., Herzog, H., and Sach, M. (1997). A pet study of cerebral activation patterns induced by verb inflection. *Neuroimage*, 5:S548.
- Indefrey, P., Brown, C. M., Hellwig, F., Amunts, K., Herzog, H., Seitz, R. J., and Hagoort, P. (2001). A neural correlate of syntactic encoding during speech production. *Proceedings of the National Academy of Sciences of the United States of America*, 98(10):5933–6.
- Jaeger, J., Lockwood, A., Kemmerer, D., van Valin, R., Murphy, B., and Khalak, H. (1996). A positron emission tomography study of regular and irregular verb morphology in English. *Language*, 72:451–497.
- Keysers, C. and Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Progress in Brain Research*, 156:379–401.
- Keysers, C., Kohler, E., Umiltà, M., Nanetti, L., Fogassi, L., and Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental Brain Research*, 153(4):628–636.
- Kilner, J. M., Friston, K. J., and Frith, C. D. (2007). The mirror-neuron system: a Bayesian perspective. *Neuroreport*, 18(6):619–23.
- Kohler, E., Keysers, C., Umiltà, M., Fogassi, L., Gallese, V., and Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297(5582):846–849.
- Koski, L., Iacoboni, M., Dubeau, M.-C., Woods, R., and Mazziotta, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of Neurophysiology*, 89(1):460–471.
- Krams, M., Rushworth, M., Deiber, M., Frackowiak, R. S., and Passingham, R. E. (1998). The preparation, execution and suppression of copied movements in the human brain. *Experimental Brain Research*, 120:386–398.
- Leiguarda, R. C. and Marsden, C. D. (2000). Limb apraxias: higher-order disorders of sensorimotor integration. *Brain*, 123 (Pt 5):860–79.
- Lieberman, A. and Mattingly, I. (1985). The motor theory of speech perception revised*. *Cognition*, 21:1–36.

- Luzzatti, C. and Bleser, R. D. (1996). Morphological processing in Italian agrammatic speakers: eight experiments in lexical morphology. *Brain and Language*, 54(1):26–74.
- Luzzatti, C., Toraldo, A., Guasti, M., Ghirardi, G., Lorenzi, L., and Guarnaschelli, C. (2001). Comprehension of reversible active and passive sentences in agrammatism. *Aphasiology*, 15(5):419–441.
- Makuuchi, M. (2005). Is Broca's area crucial for imitation? *Cerebral Cortex*, 15(5):563–70.
- Meyer, M., Friederici, A. D., and von Cramon, D. Y. (2000). Neurocognition of auditory sentence comprehension: event related fMRI reveals sensitivity to syntactic violations and task demands. *Cognitive Brain Research*, 9(1):19–33.
- Miceli, G., Silveri, M. C., Villa, G., and Caramazza, A. (1984). On the basis for the agrammatic's difficulty in producing main verbs. *Cortex*, 20(2):207–20.
- Morin, O. and Grèzes, J. (2008). What is "mirror" in the premotor cortex? a review. *Neurophysiologie clinique = Clinical neurophysiology*, 38(3):189–95.
- Nishitani, N. and Hari, R. (2000). Temporal dynamics of cortical representation for action. *Proceedings of the National Academy of Sciences of the United States of America*, 97(2):913–8.
- Passingham, R. (1993). The frontal lobes and voluntary action. *Oxford University Press*.
- Passingham, R. E. (1981). Broca's area and the origins of human vocal skill. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 292(1057):167–75.
- Pazzaglia, M., Smania, N., Corato, E., and Aglioti, S. M. (2008). Neural underpinnings of gesture discrimination in patients with limb apraxia. *The Journal of Neuroscience*, 28(12):3030–41.
- Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., and Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91:176–180.
- Petrides, M. (2006). Broca's area in the human and nonhuman primate brain. In Grodzinsky, Y., editor, *Broca's region*. Oxford University Press.

- Petrides, M. and Pandya, D. (1994). Comparative cytoarchitectonic analysis of the human and the macaque frontal cortex. *Handbook of neuropsychology*, 9:17–58.
- Pick, A. (1898). Über agrammatismus als folge cerebraler herderkrankungen; ein beitrage zur lehre vom verhältnis der worttaubheit. *Beiträge zur Pathologie und pathologischen Anatomie des ZentralNervensystems*, 9:123–133.
- Pick, A. (1913). *Die agrammatischen Sprachstörungen. Studien zur psychologischen Grundlegung der Aphasielehre. Teil I*. Berlino: Springer.
- Pobric, G. and de C Hamilton, A. F. (2006). Action understanding requires the left inferior frontal cortex. *Current biology*, 16(5):524–9.
- Renzi, E. D., Motti, F., and Nichelli, P. (1980). Imitating gestures - quantitative approach to ideomotor apraxia. *Archives of Neurology*, 37(1):6–10.
- Rizzolatti, G. and Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, 21(5):188–194.
- Rizzolatti, G. and Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27:169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996a). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3(18):131–141.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., and Fazio, F. (1996b). Localization of grasp representations in humans by pet: 1. observation versus execution. *Experimental Brain Research*, 111(2):246–252.
- Rossi, E. and Bastiaanse, R. (2008). Spontaneous speech in italian agrammatic aphasia: A focus on variability and verb production. *Aphasiology*, 22:347–362.
- Saygin, A., Wilson, S. M., Dronkers, N. F., and Bates, E. (2004). Action comprehension in aphasia: linguistic and non-linguistic deficits and their lesion correlates. *Neuropsychology*, 42(13):1788–804.
- Schubotz, R. I. and von Cramon, D. Y. (2001). Functional organization of the lateral premotor cortex: fmri reveals different regions activated by anticipation of object properties, location and speed. *Cognitive Brain Research*, 11(1):97–112.
- Schubotz, R. I. and von Cramon, D. Y. (2002a). A blueprint for target motion: fmri reveals perceived sequential complexity to modulate premotor cortex. *Neuroimage*, 16(4):920–35.

- Schubotz, R. I. and von Cramon, D. Y. (2002b). Dynamic patterns make the premotor cortex interested in objects: influence of stimulus and task revealed by fmri. *Cognitive Brain Research*, 14(3):357–69.
- Schubotz, R. I. and von Cramon, D. Y. (2002c). Predicting perceptual events activates corresponding motor schemes in lateral premotor cortex: an fmri study. *Neuroimage*, 15(4):787–96.
- Schubotz, R. I. and von Cramon, D. Y. (2003). Functional-anatomical concepts of human premotor cortex: evidence from fmri and pet studies. *Neuroimage*, 20 Suppl 1:S120–31.
- Seitz, R. J. and Roland, P. (1992). Learning of sequential finger movements in man: A combined kinematic and positron emission tomography (pet) study. *The European Journal of Neuroscience*, 4(2):154–165.
- Shapiro, L. and Levine, B. (1990). Verb processing during sentence comprehension in aphasia. *Brain and Language*, 38:21–47.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, E., Rizzolatti, G., Cappa, S. E., and Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, 17(2):273–81.
- Tranel, D., Kemmerer, D., Adolphs, R., and Damasio, H. (2003). Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology*, 20:409–432.
- von Bonin, G. and Bailey, P. (1947). *The neocortex of Macaca mulatta*. Illinois: The University of Illinois Press,.
- von Bonin, G. and Bailey, P. (1961). Pattern of the cerebral isocortex. In Hofer, H., Schulz, A., and Starck, D., editors, *Primatologia*; pages 1–42 Part 2, Lieferung 10. Karger, Basel.
- Zingeser, L. B. and Berndt, R. S. (1990). Retrieval of nouns and verbs in agrammatism and anomia. *Brain and Language*, 39(1):14–32.

