The neurophysiology of language and the nature / culture dyad

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Nature / Culture

according to traditional philosophic views, there is a clear-cut separation between nature and culture;

- a number of natural properties determine structures and functions that humans and animals share;
- however, mankind-specific behaviors and products are linked to what we call culture, including language.

Nature / Culture

what is the input of neurophysiology (and cognitive neurosciences) to the classical debates

- on the ‘natural bases’ of language ?
- on the irreducible uniqueness of the human culture, relative to sophisticated behaviors discovered in some animal societies ?

SUR LE SIÉGE

DE LA

FACULTÉ DU LANGAGE ARTICULÉ

DIT AUX OBSERVATIONS

D'APHÉMIE

(PERTE DE LA PAROLE)

PAR LE Dr PAUL BROCA

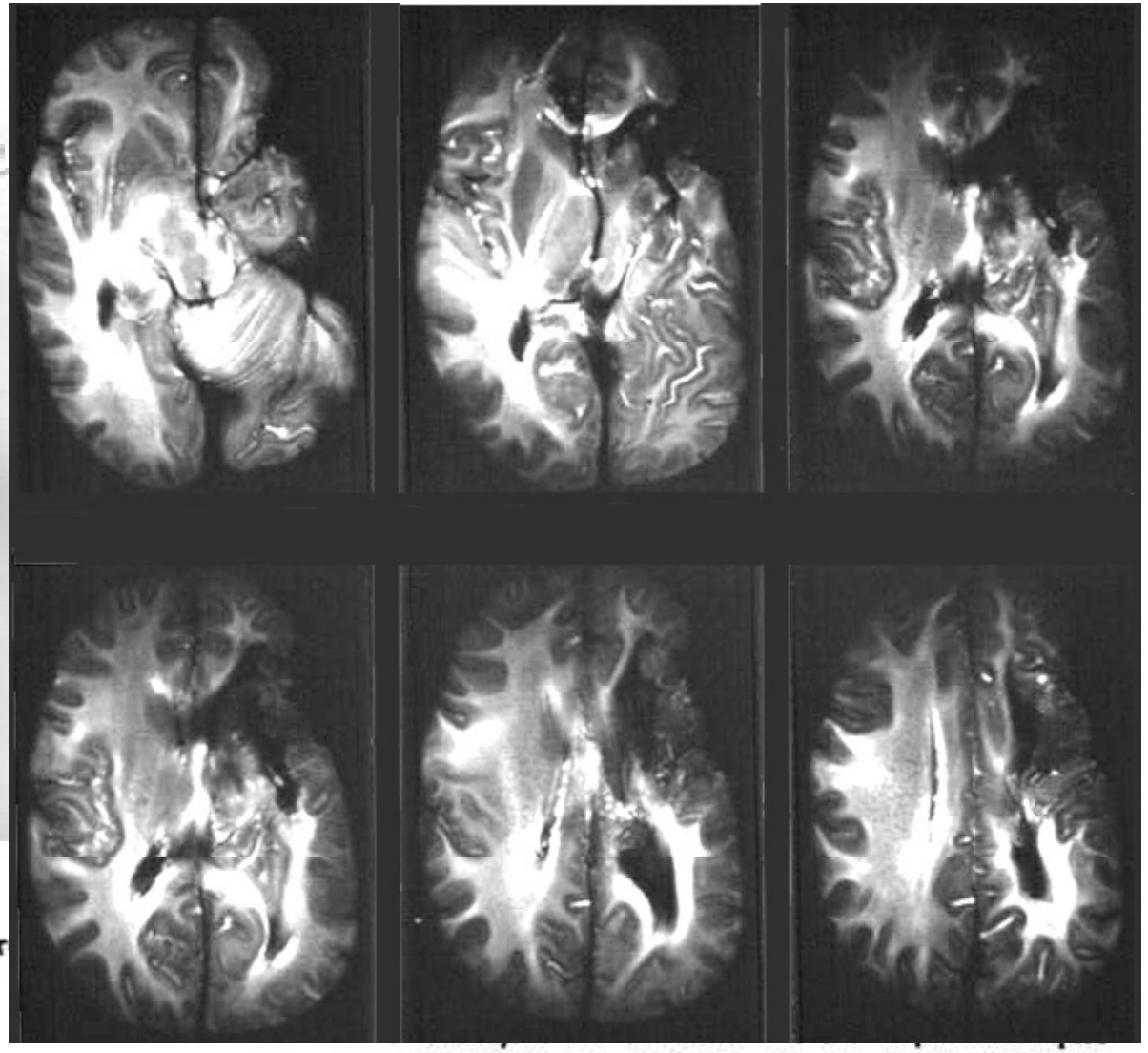
Professeur agrégé à la Faculté de médecine, chirurgien de l'hôpital de Bicêtre.

PARIS

VICTOR MASSON ET FILS

PLACE DE L'ÉCOLE-DE-MÉDECINE

1861

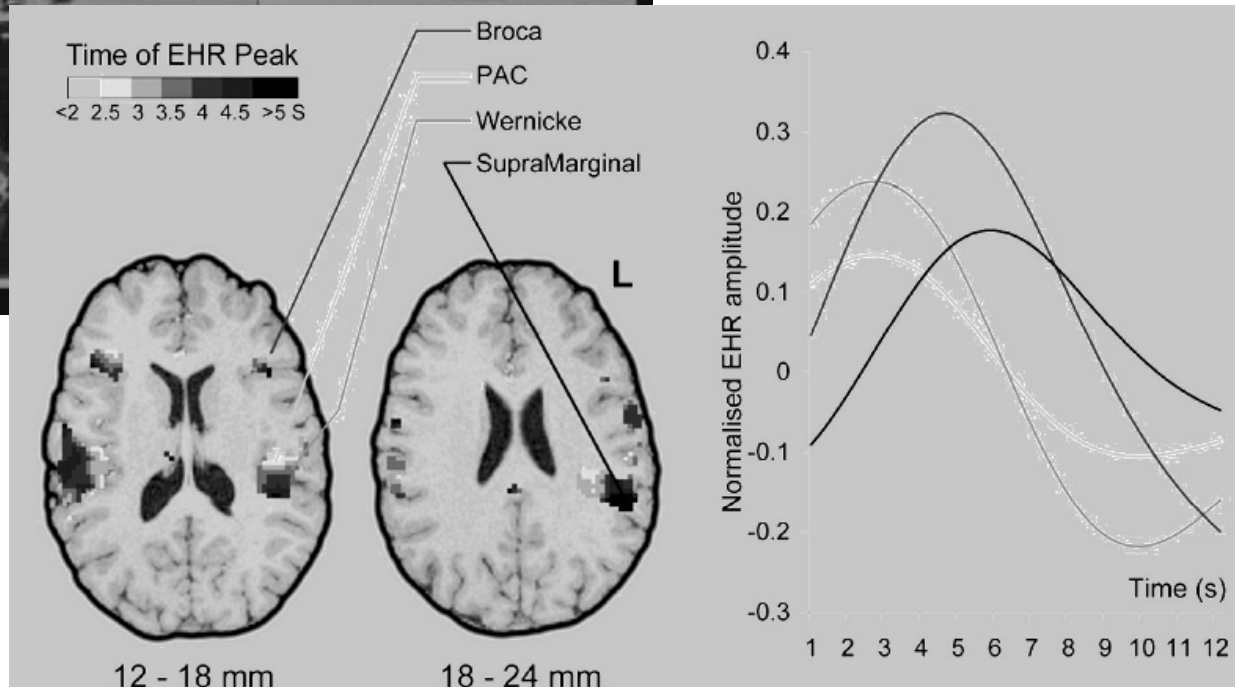


Deuxième période (onze ans)	*a*. Propagation au corps strié gauche.	Paralysie croisée du mouvement.
	b. Ramollissement de tout le lobe frontal gauche; atrophie générale des hémisphères	Affaiblissement de l'intelligence.

the « nature » of language: brain imaging

the neurophysiology of language

Physiol. Rev. 2005)



the nature of the culture

Culture may be defined, in a group of individuals, as a social phenomenon that relates to a complex set of mental representations, behaviors, conventions, activities, artefacts, products, … ; these social phenomena are

- modified/enriched via individual experience
- shared among individuals belonging to a particular group
- transmitted to the next generations
- represented at a meta-cognitive level in members of the group: i.e. individual subjects who are supposed to experience inner mental states, intentions and feelings, (i) can form mental representations of culture elements, (ii) can communicate with congeners on these second-order representations

While all these criteria are jointly met only in human societies, there are examples of animal groups in which some behaviors comply partly with this multi-item definition

Examples of sophisticated communication abilities in animal species (general reference M. Hauser: 1996)

- The famous case of the development of song abilities in some bird species (Marler, 1970): perhaps not so well-known are the massive influence of the social interactions with adults and of adult songs to which young birds are exposed (e.g. the richness of ”teachers” song modulates the duration of the critical period for song development: Brainard, 1998 and Baptista, & Petrinovich 1986)
- Also very well-known are the observations and experiments on rudiments of language that great apes bonobos can manage (Savage-Rumbaugh, De Waal and Lenting 1997)

Examples of sophisticated communication abilities in animal species (continued)

- in many animal societies, at least in vertebrates, game plays a major social role; in chimpanzees, specific signs have been identified that denote and ‘announce’ that the ‘signer’ is about to begin playing; this announcing signs witness second-order evaluation of behavior and imply metacognitive representations (re: G. Bateson);
- more recent and experimental evidence of metacognitive abilities have accumulated in macaques: e.g. when the animal seems to ‘put a bet’ on the accuracy of its own performance on a working memory task (Kornell et al. 2007)

http://www.columbia.edu/cu/psychology/primatecognitionlab/

the nature of the culture: the case of language

- Humans use different sensory-motor channels to communicate between conspecifics; however language is the most efficient of these communication means.
- From the point of view of physiology, language may be viewed as a « natural product » resulting from specific activities in an individual's brain;
- However, from the point of view of anthropology, (i) language is both a hall-mark of the human culture and the most powerful way to disseminate this culture throughout human groups

the nature of the culture: the case of language (c'ed)

(ii) language is not an isolated entity; it is rather linked to inter-individual communication and cultural specificities:

- young humans develop spoken language only in a social context; therefore, brain networks linked to language are unlikely to be independent of neural structures supporting other communication functions and social interactions;

(ii) human cultures by themselves, and especially features of specific languages, can reshape neural activities in brain networks innately independent of culture (e.g. the left fusiform cortex and reading,

S. Dehaene & L. Cohen)

Theoretical frameworks for studying the brain correlates of language

* Psycholinguistics

- **hierarchical organisation of linguistic structures : phoneme, lexicon, …**
- **Rule / Lexicon** (e.g. Ullman et al. 1997)
- Syntax
- Prosody ? (e.g. *Magne et al 2005*)
- Pragmatics ? (understanding metaphors, e.g. Bottini et al 1994)

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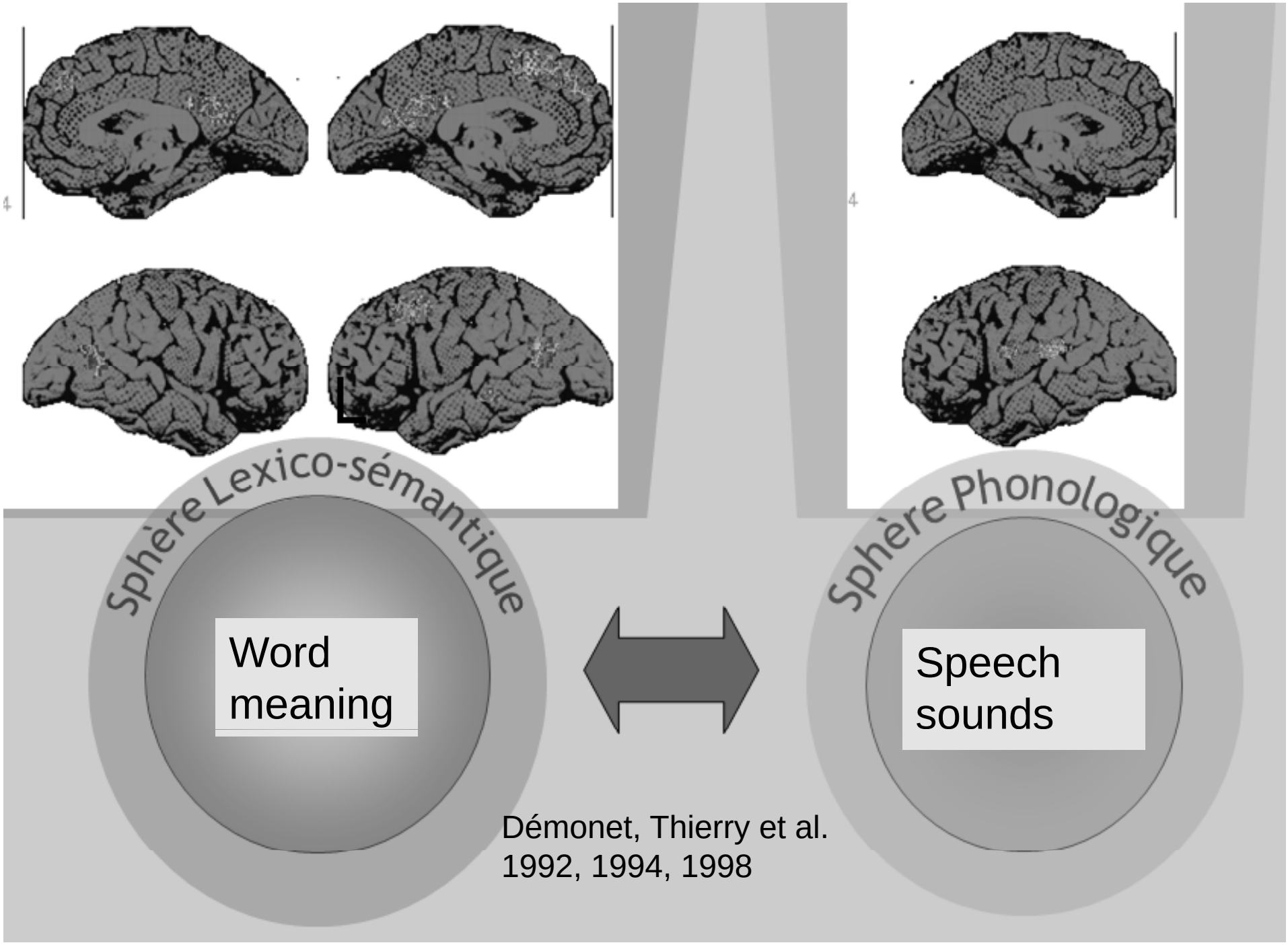
Sphère Lexico-sémantique
Word meaning
Sphère Phonologique
Speech sounds
Démonet, Thierry et al.
1992, 1994, 1998

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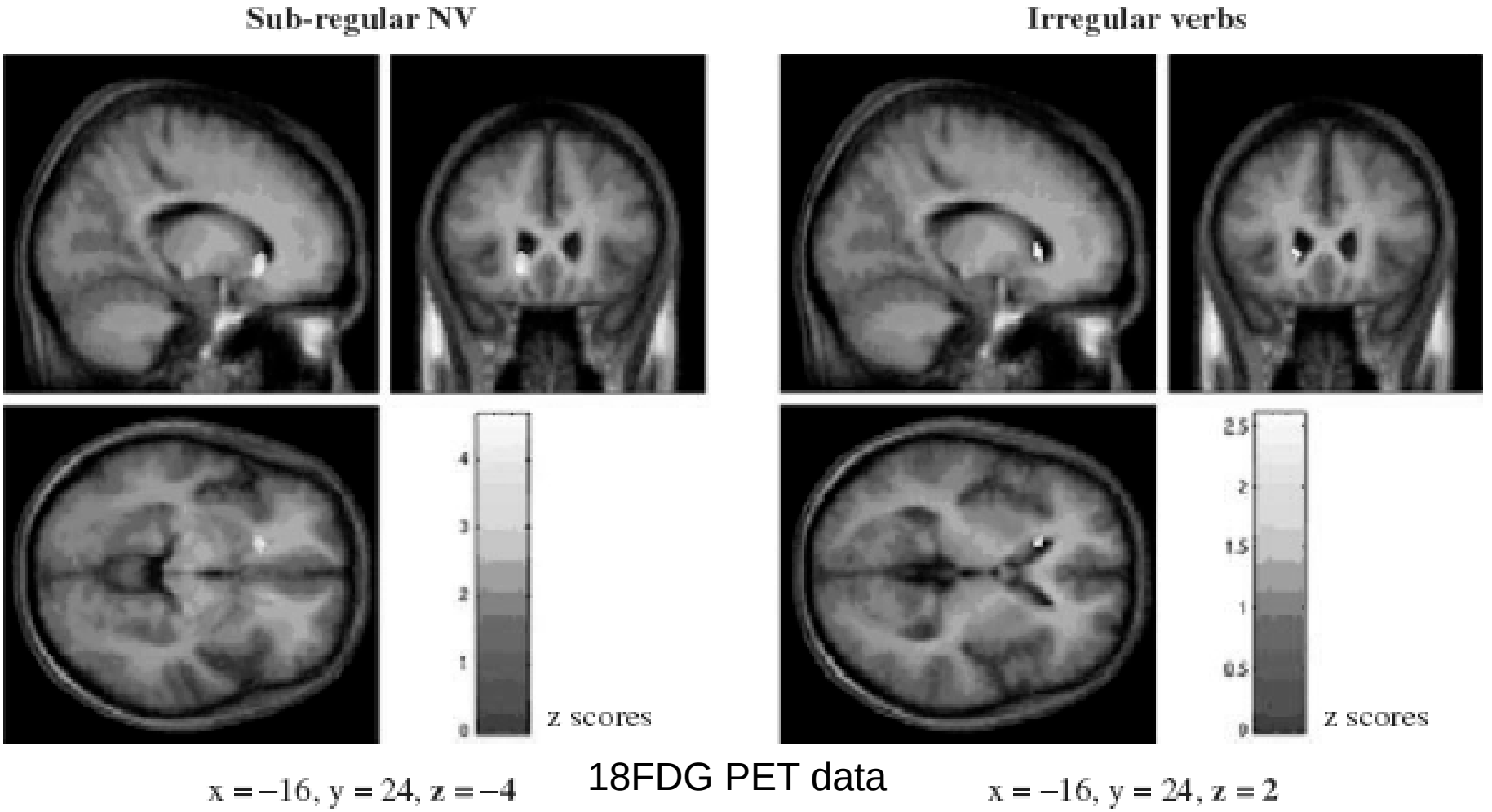
- Pragmatics ?

In patients with Huntington's disease which affects primarily the striatum , language performance were correlated with neural activity : different parts of the striatum were linked to either rule-based processing or lexical access



18FDG PET data

Teichmann et al., 2008

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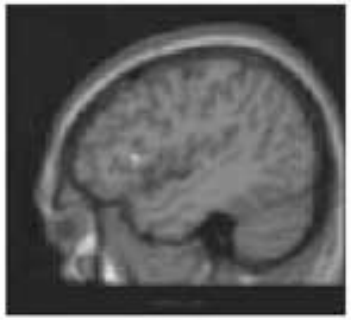
- Pragmatics ?

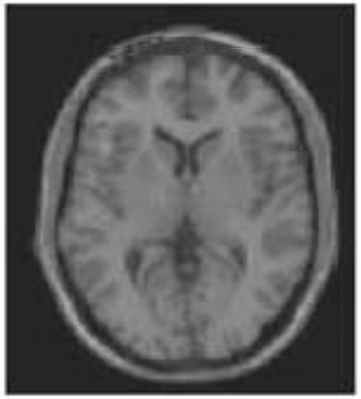
Broca's area and learning of syntax rules

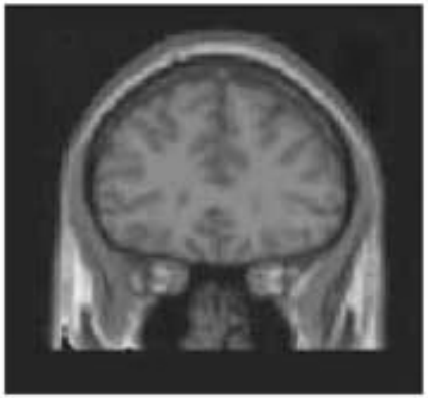
rules that either tie up to the « universal grammar » principles (Chomsky) or were arbitrarily designed

Musso et al., *Nature*, 2003

Results waiting for replication

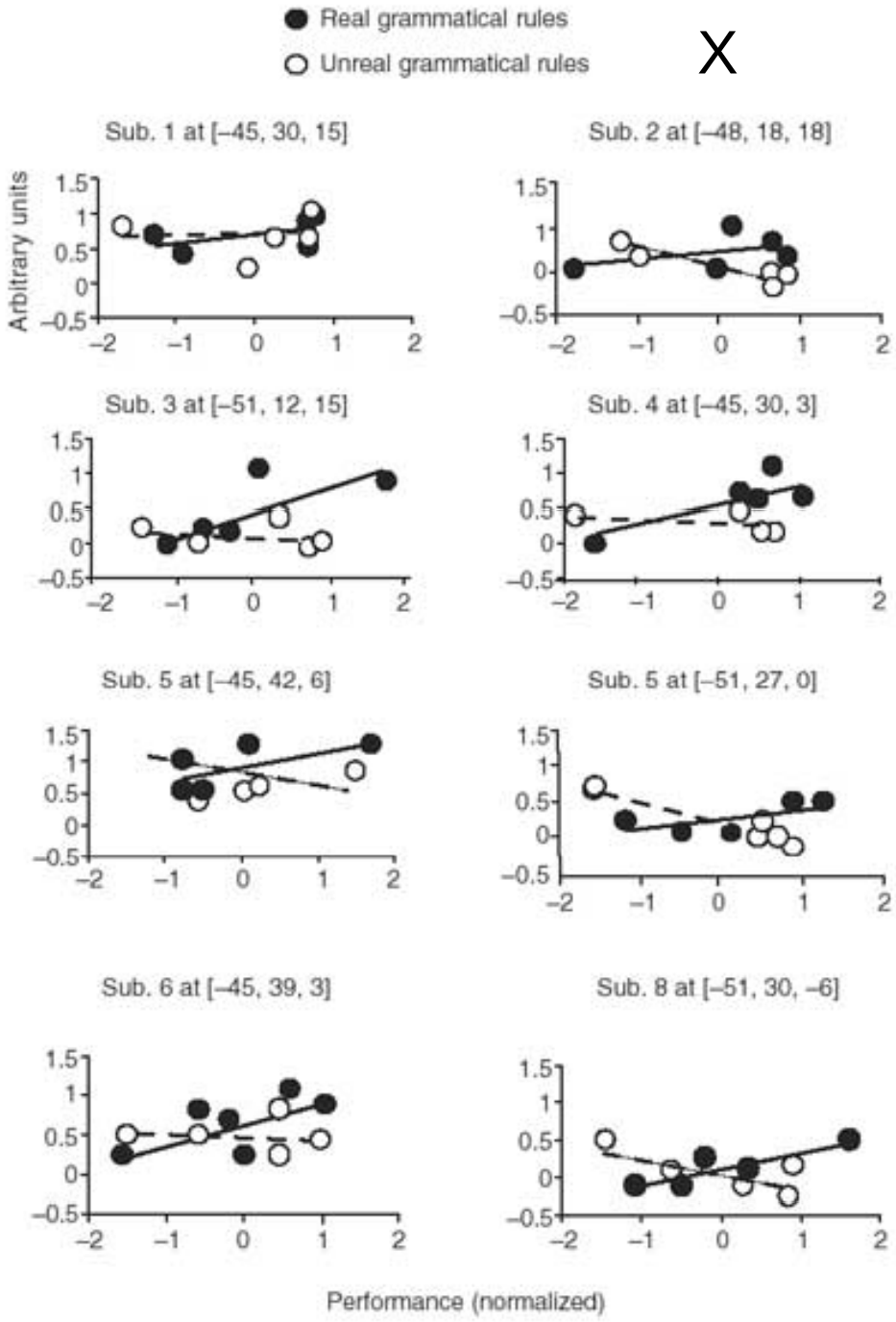




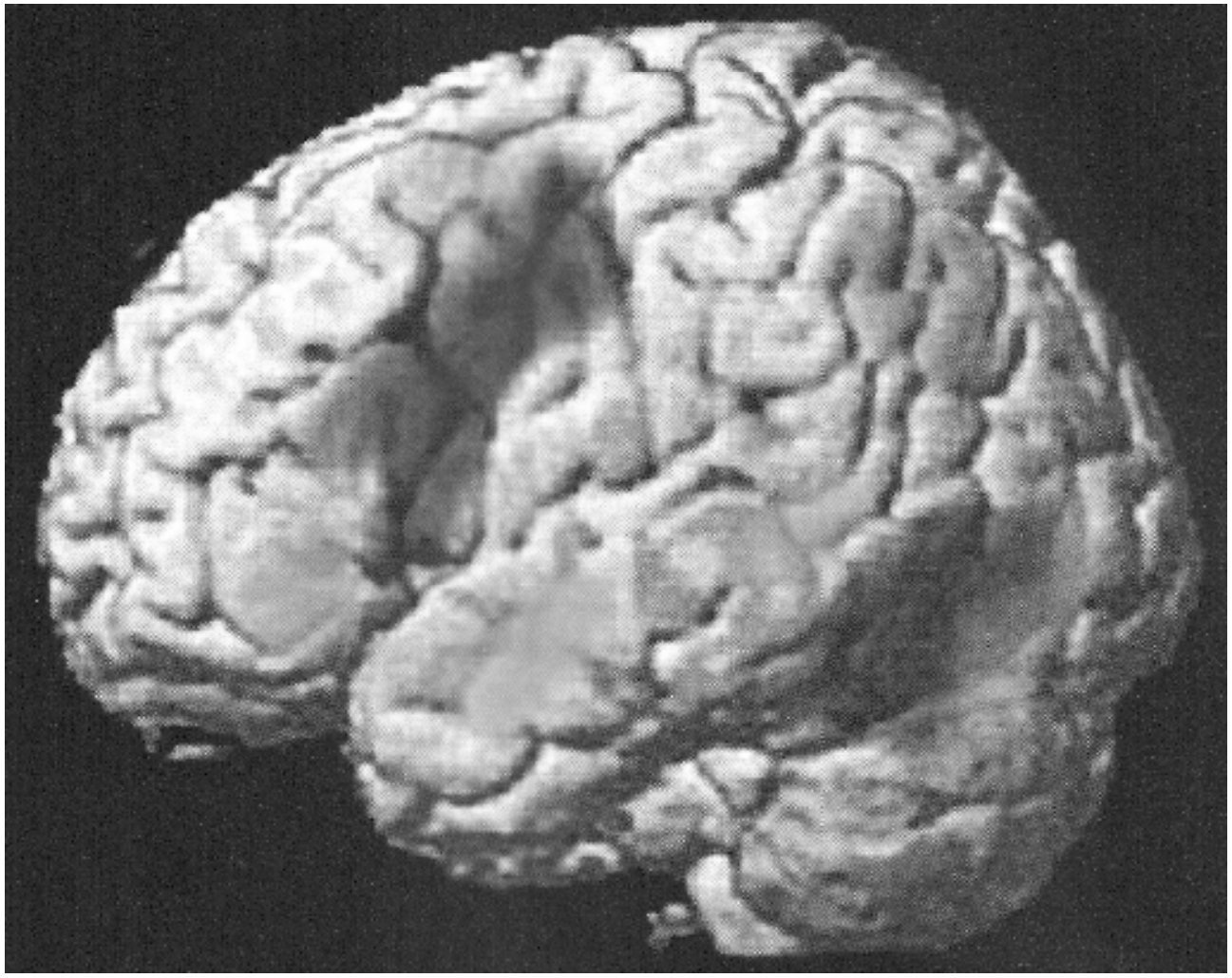


[–45, 21, 6] Italian experiment (yellow)
[–45, 33, 3] Japanese experiement (red)

X



Questioning the specificity of the syntactic nature of observed effects



Hoehn and Dominey, *Cortex*, 2006

Sequences & Sentences

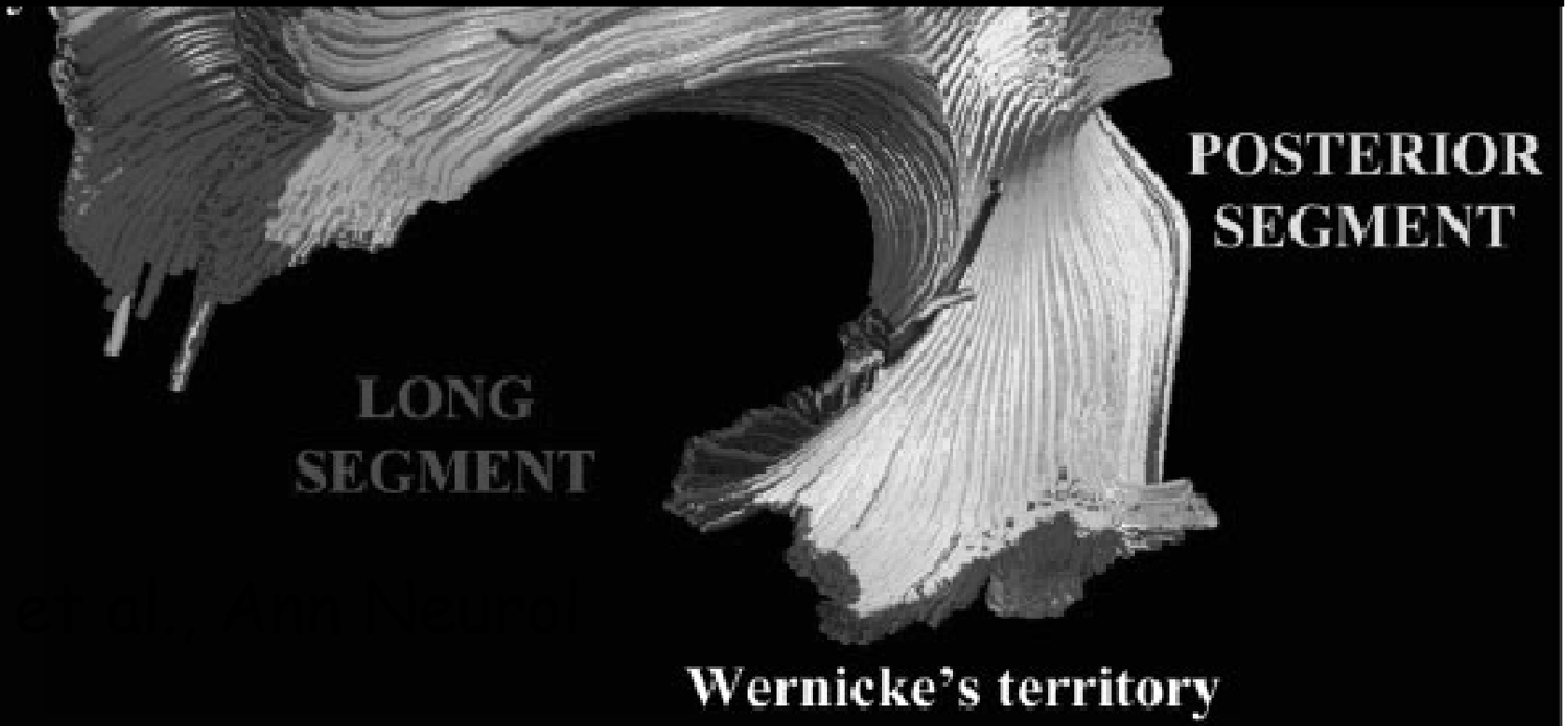
right hemisphere: similar pattern, weaker activation

Sentences > Sequences

right hemisphere: lingual gyrus, middle temp gyrus

Theoretical frameworks for studying the brain substrates of language

* Neurophysiology



Theoretical frameworks for studying the brain correlates of language

* Neurophysiology

- **Ventral / Dorsal**

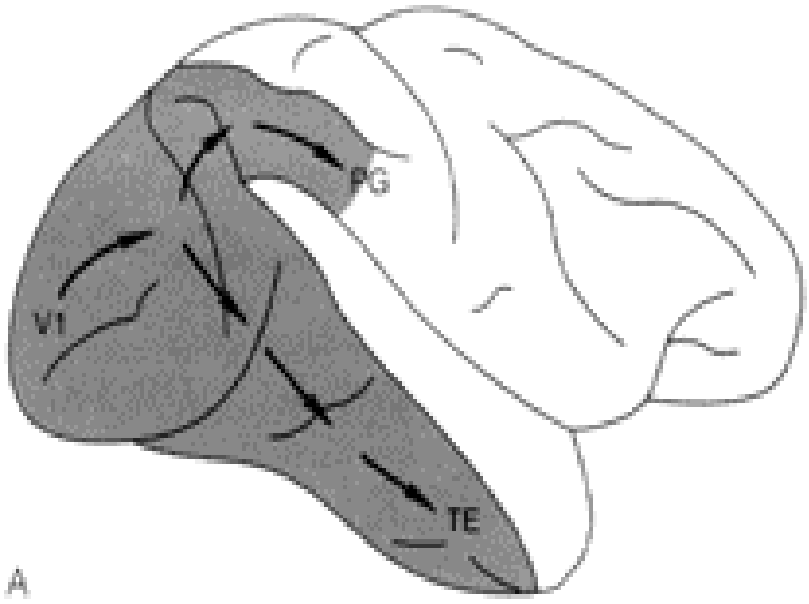
- **Mirror neurons:**

re: social cognition ?

nature

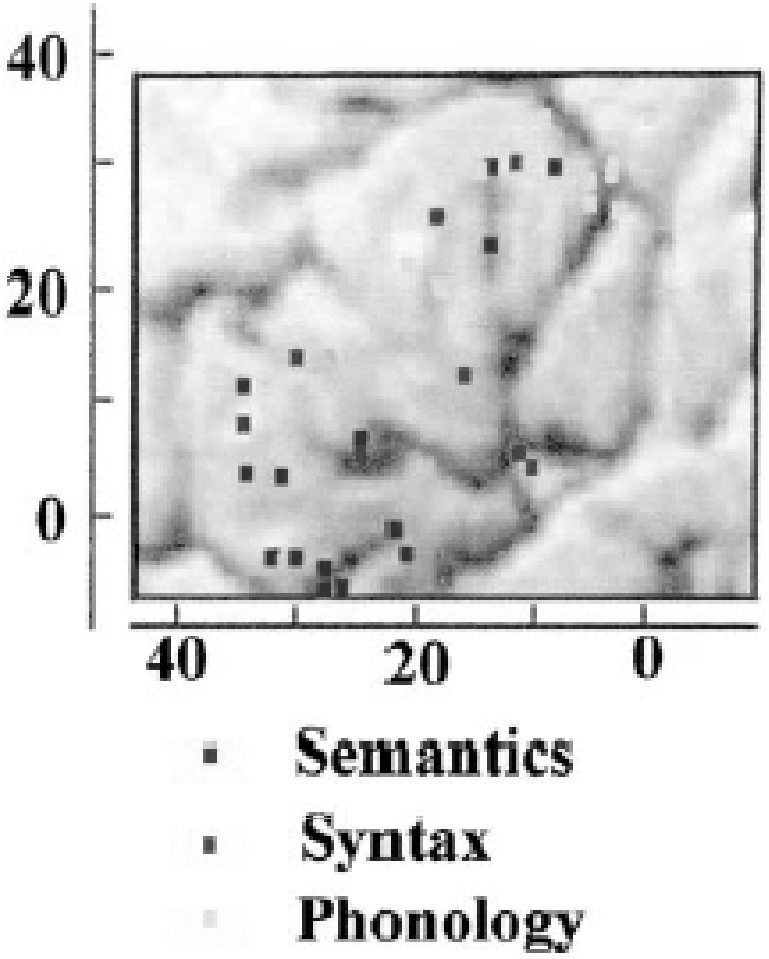
The ventral / dorsal segregation of processing

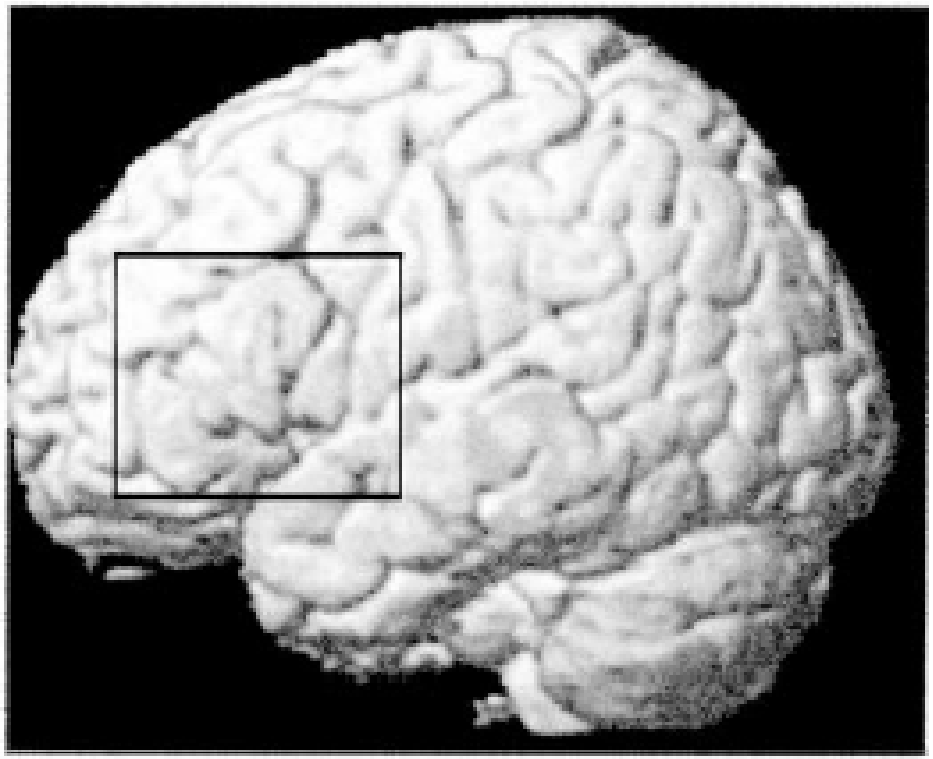
- ventral stream: linked to recognition of LTM contents and semantic processing
- dorsal stream: in charge of on-line sequence decoding and recombining sequences in working memory, linked to phonological and syntaxic processing



from Ungerleider et Mishkin, 1982

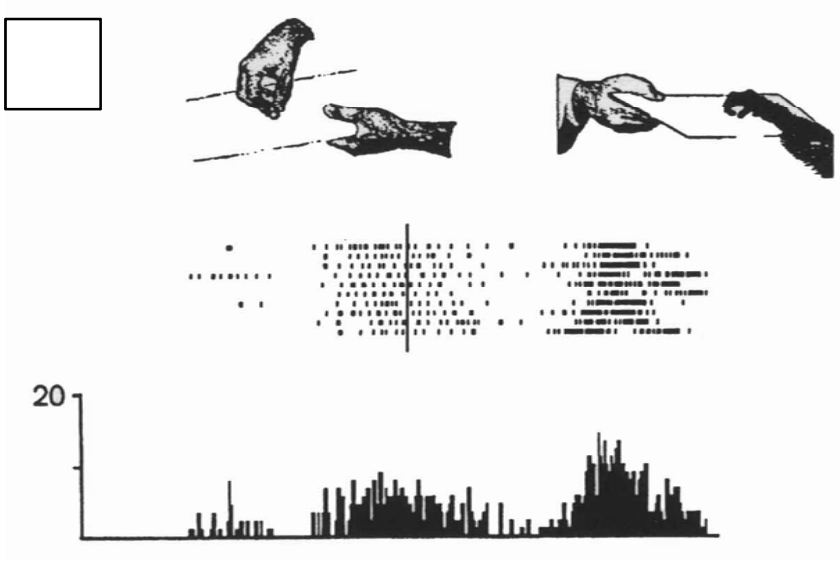
Bookheimer Ann Rev Neurosci 2002



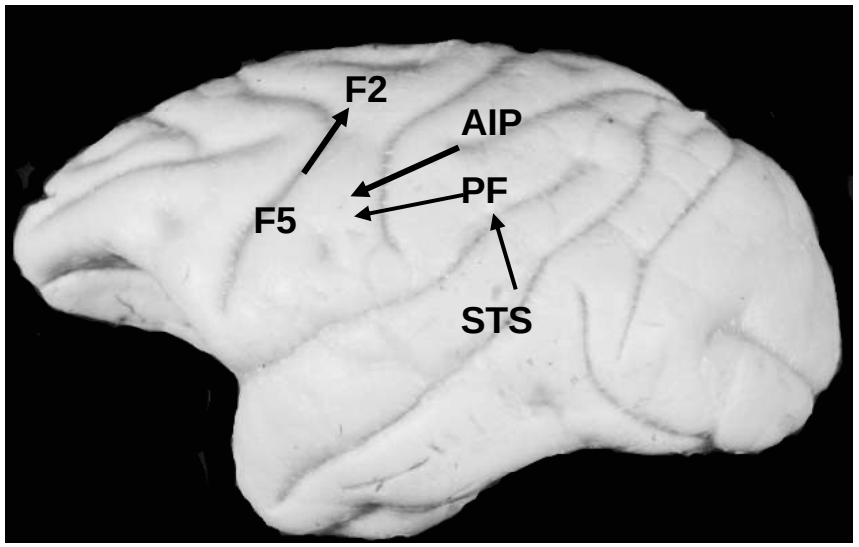


Mirror neurons

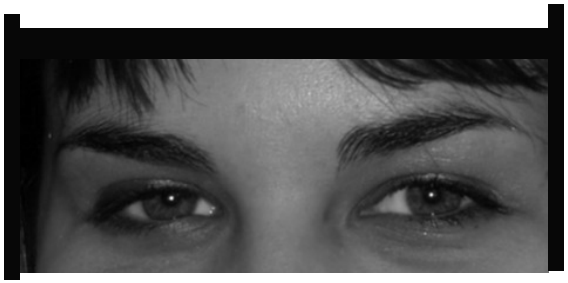
First observed in macaque monkeys as particular visual properties of neurons in F5 area



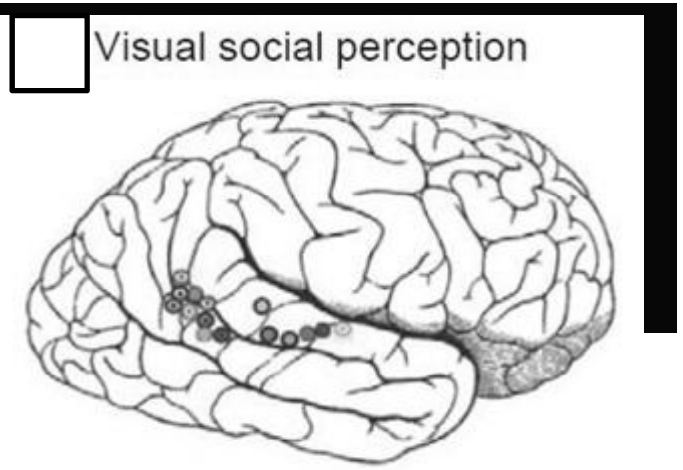
Di Pelligrino et al. (1992)

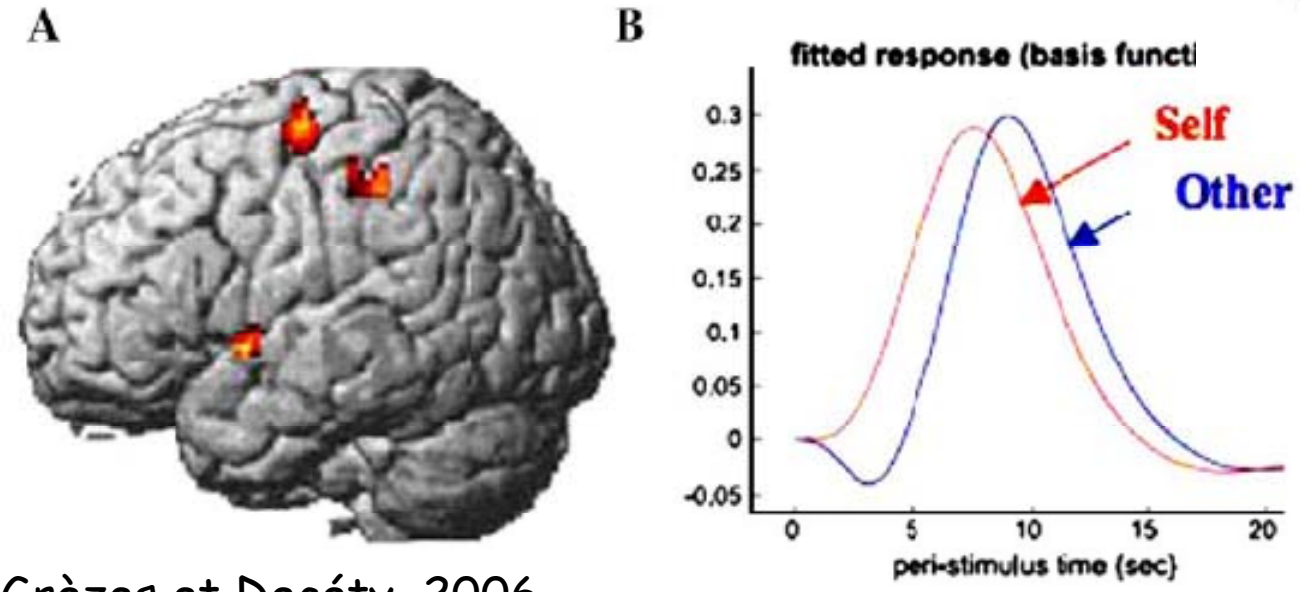


Neurons are active both upon monkey's own movement and upon observation of another individual executing the same action.



STS, « theory of mind » and
the brain substrates
of inter-individual communication
Role of mirror neurons ?





Grèzes et Decéty, 2006

Social cognition and language

« Human language provides an opportunity to study the interface between systems that control the acquisition of complex behavioral repertoires in natural social settings » (P. Khul, *PNAS*, 2003)

The nature of spoken language

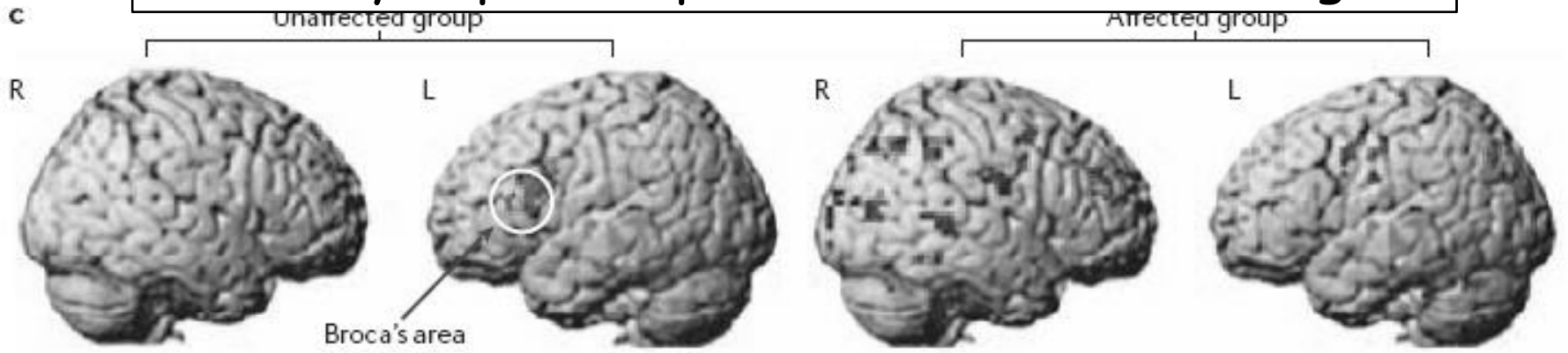
genetic bases

The eloquent ape: genes, brains and the evolution of language

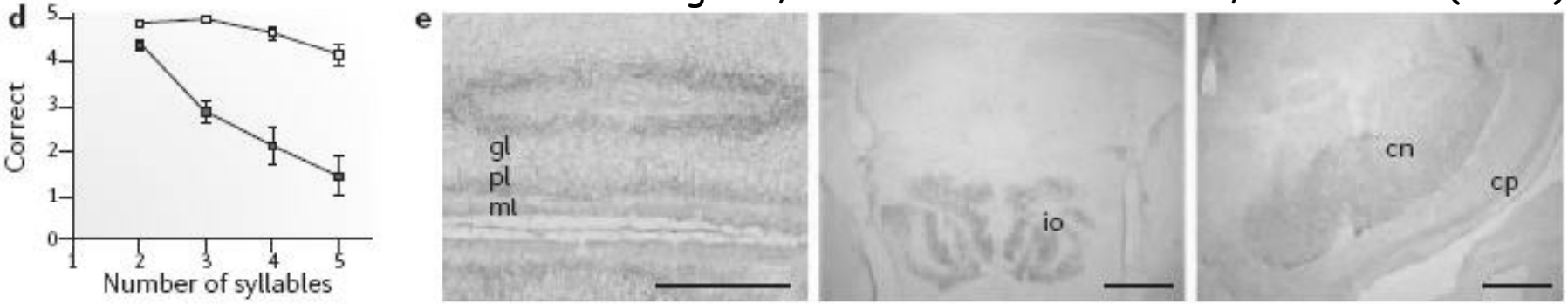
Simon E. Fisher and Gary F. Marcus‡*

Nature Reviews Genetics Jan 2006

KE family: speech apraxia , mutated FoxP2 gene



Liégeois, *et al. Nature Neurosci.* **6**, 1230–1237 (2003)

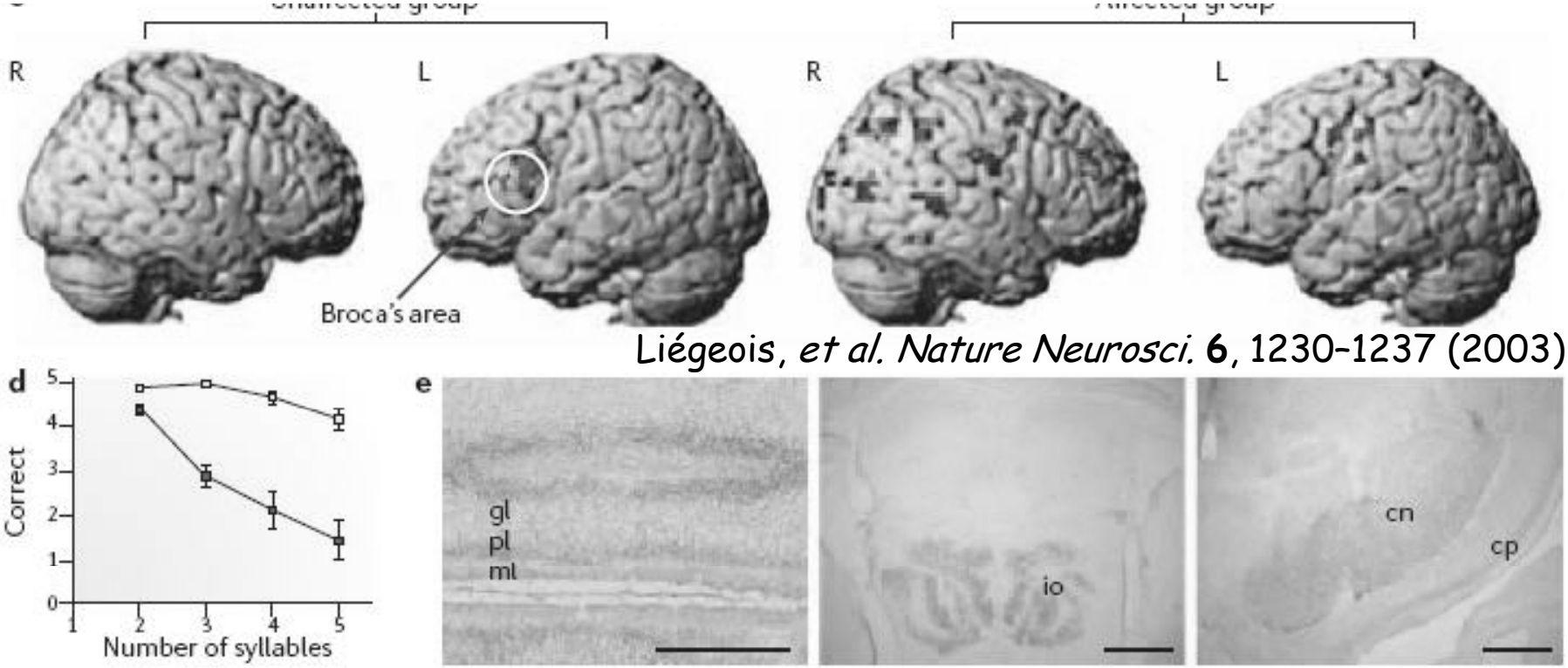


FoxP2 has an important role in the development of the frontal cortex, striatum, cerebellum; in some bird species, expression peak of FoxP2 observed in the critical periods of song adaptation

ARTICLE

Identification of the Transcriptional Targets of *FOXP2*, a Gene Linked to Speech and Language, in Developing Human Brain

Elizabeth Spiteri, Genevieve Konopka, Giovanni Coppola, Jamee Bomar, Michael Oldham, Jing Ou, Sonja C. Vernes, Simon E. Fisher, Bing Ren, and Daniel H. Geschwind

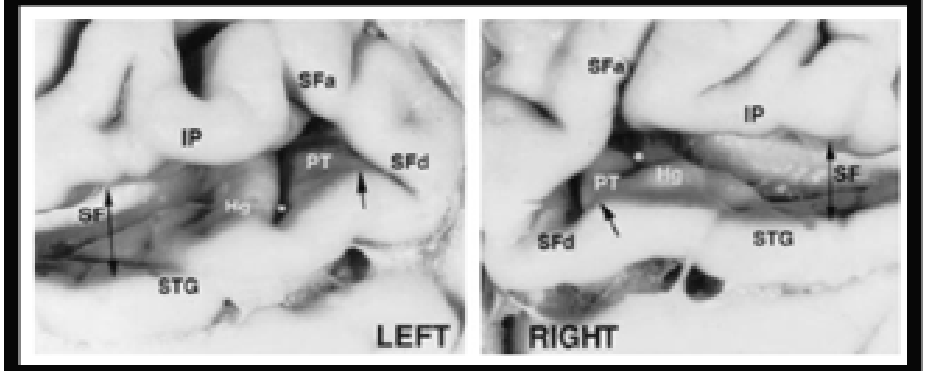


Liégeois, *et al. Nature Neurosci.* **6**, 1230–1237 (2003)

FoxP2 transcriptional target genes EFNB3, HESX1, and CER1, in human foetal brain (inferior frontal gyrus and basal ganglia); genes possibly involved in **neurite growth, calcium signalling and neural plasticity**;

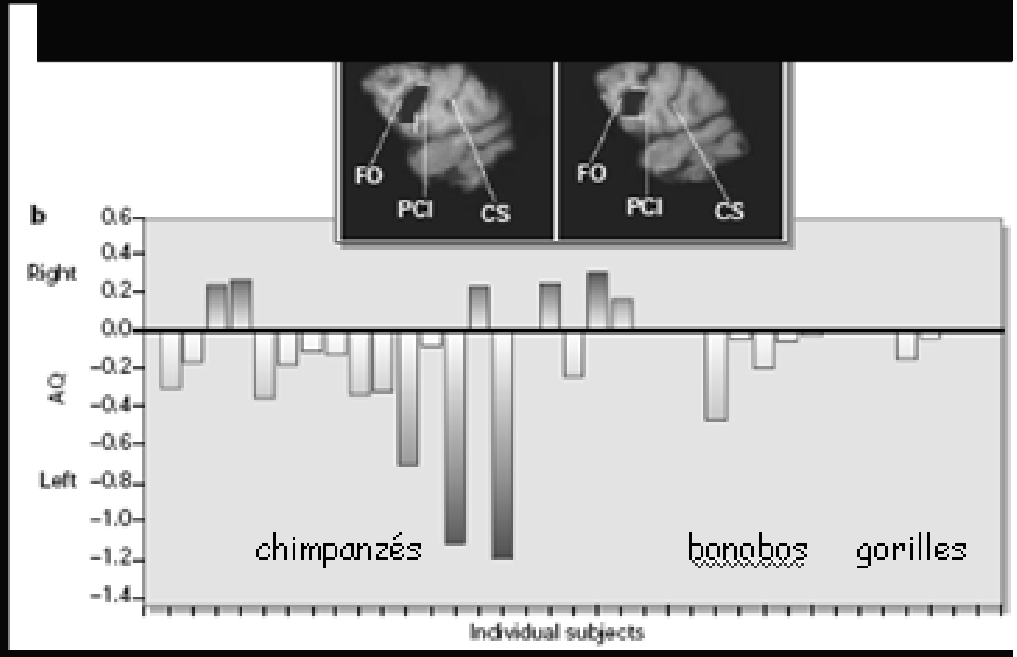
The nature of spoken language: areas in monkey brains homolog to language areas

Assymetry of the planum temporale



Gannon et al., 1998

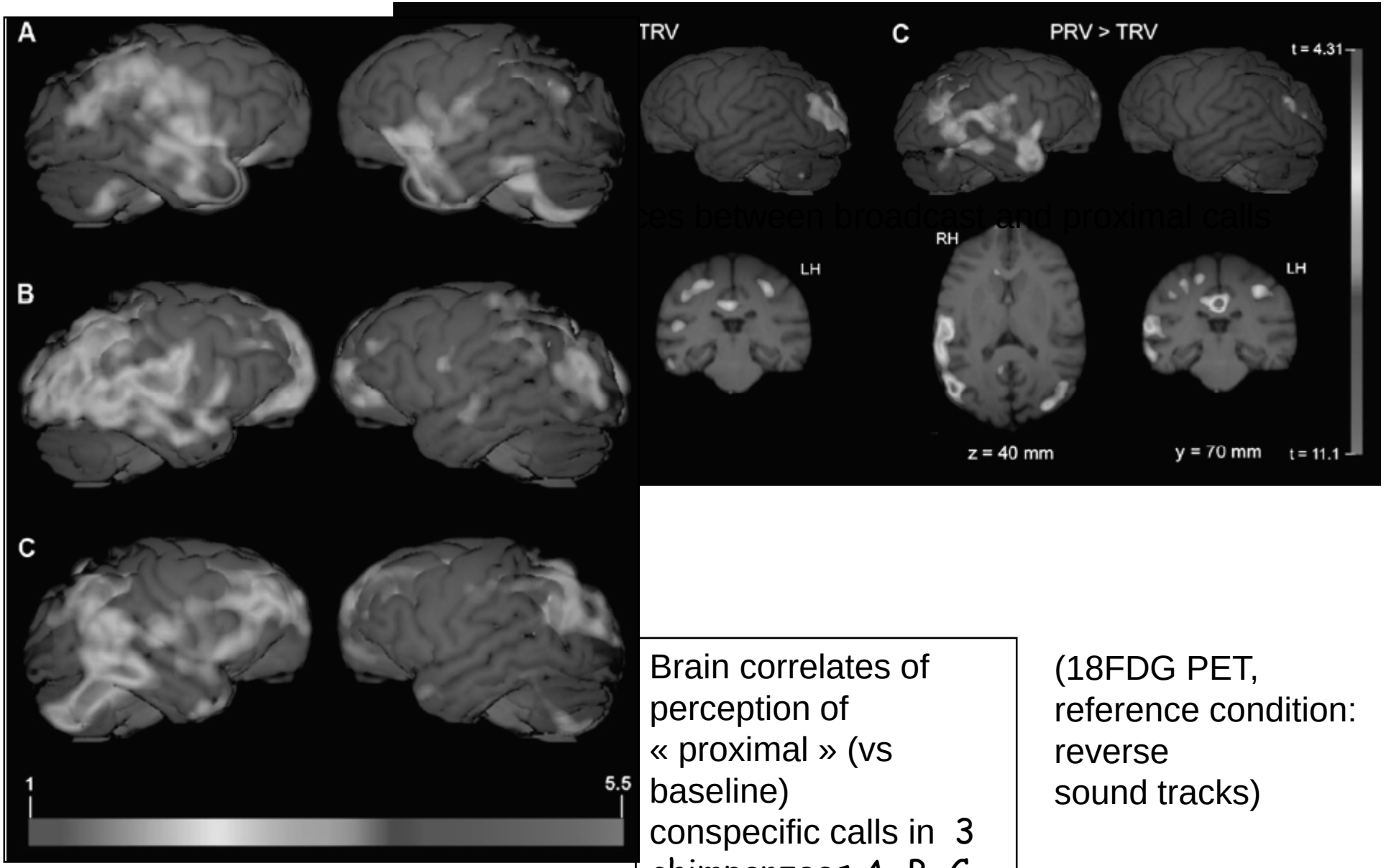
Assymetry of the inferior frontal cortex



Cantalupo et Hopkins, 2001

The nature of spoken language:

perception of conspecific calls in great apes (Taglialatela et al., 2008)



Brain correlates of perception of « proximal » (vs baseline) conspecific calls in 3 chimpanzees A, B, C

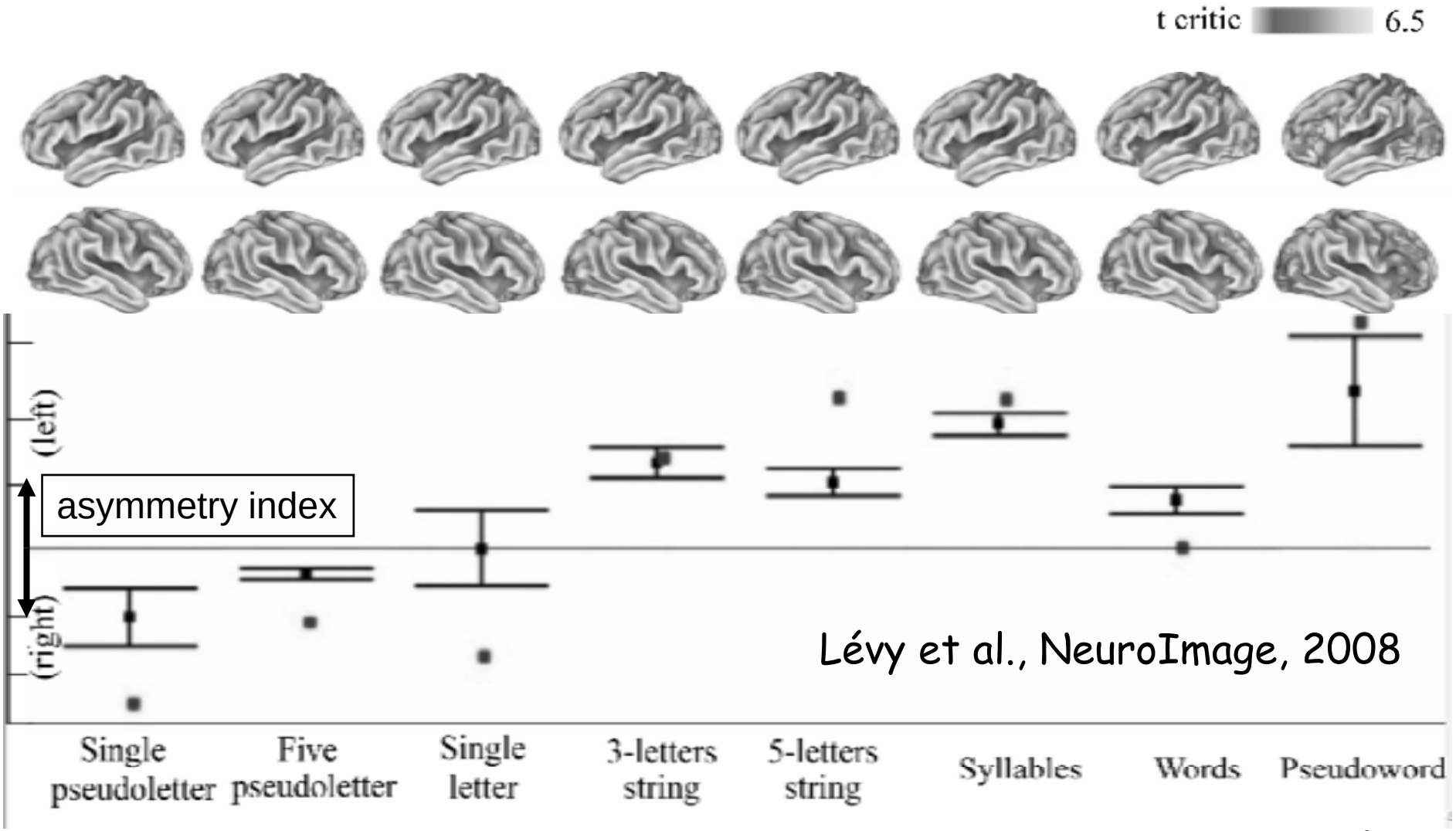
(18FDG PET, reference condition: reverse sound tracks)

Culture: the case of written language

From the point of view of anthropology, the advent of written language has been a major step forward for mankind as it makes it possible that communication gets rid of time and space constraints

From the point of view of cognitive neuroscience, unlike spoken language, reading and writing abilities only develop with explicit teaching;

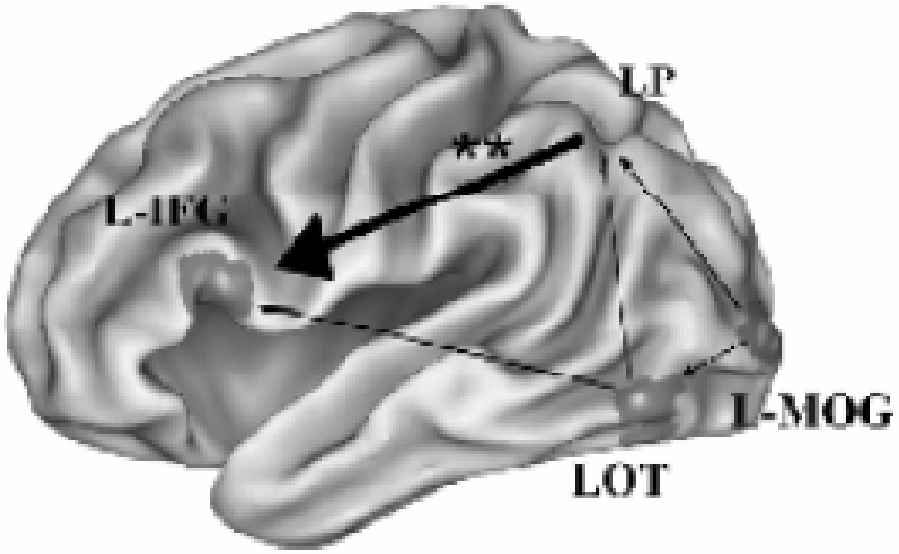
the visuo-(ortho)graphic system is a « cultural » function, superimposed on the « natural » spoken language system (cf. Dehaene's formulation of « recycling » of function of some otherwise specialized cortical territories)


t critic
6.5
(left)
asymmetry index
(right)
Lévy et al., NeuroImage, 2008
Single pseudoletter
Five pseudoletter
Single letter
3-letters string
5-letters string
Syllables
Words
Pseudoword
Increasing processing load

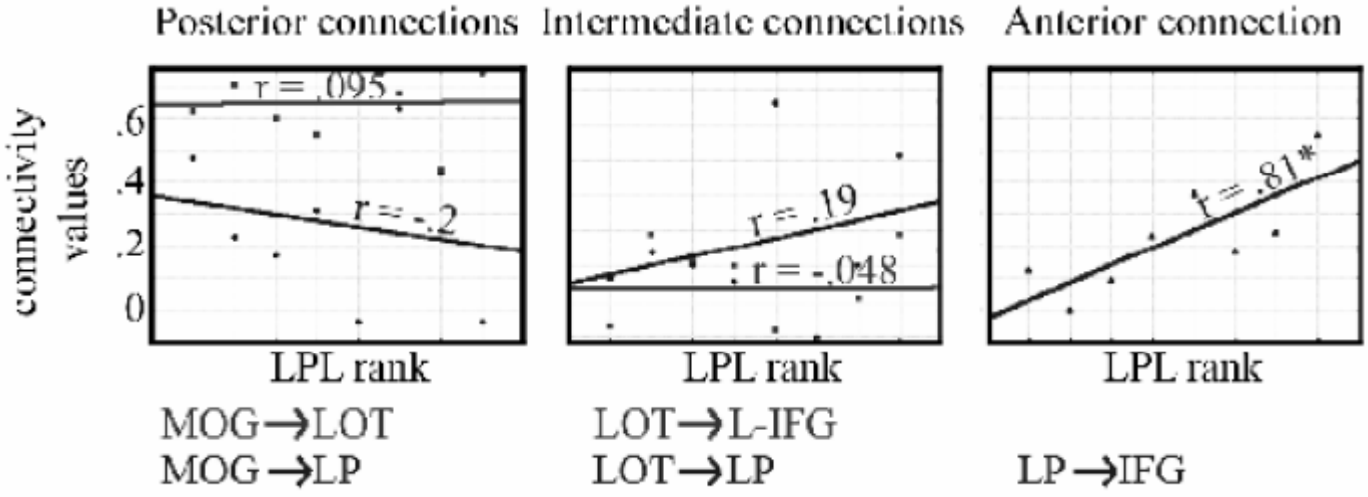
Visual symbolic processing in apes

Chimpanzees can learn to label sets of real-life objects with
arabic numerals and to process numbers in the correct order in a working memory task
(Matsuzawa and colleagues, Nature 1985, Curr Biol 2007)
http://www.pri.kyoto-u.ac.jp/koudou-shinkei/shikou/chimphome/video/video_library/project/project.html

effective connectivity analysis



Lévy et al.
Neuroimage
2008



Passive viewing of orthographic stimuli with increasing complexity (visual stimuli with constant size)

culture

(il)literacy effects

literates

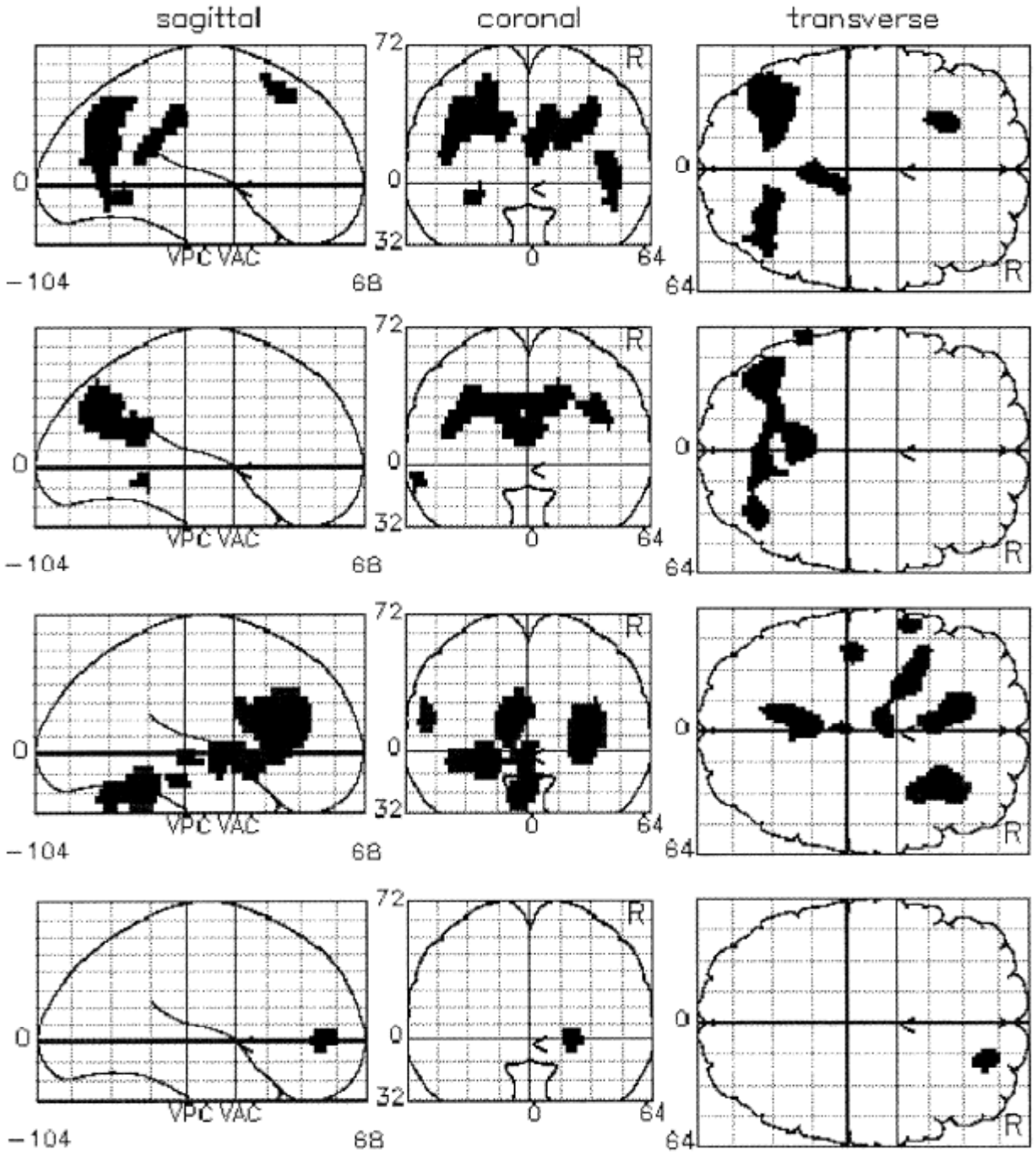
Word repetition (against pseudowords)

illiterates

literates

Pseudoword repetition (against words)

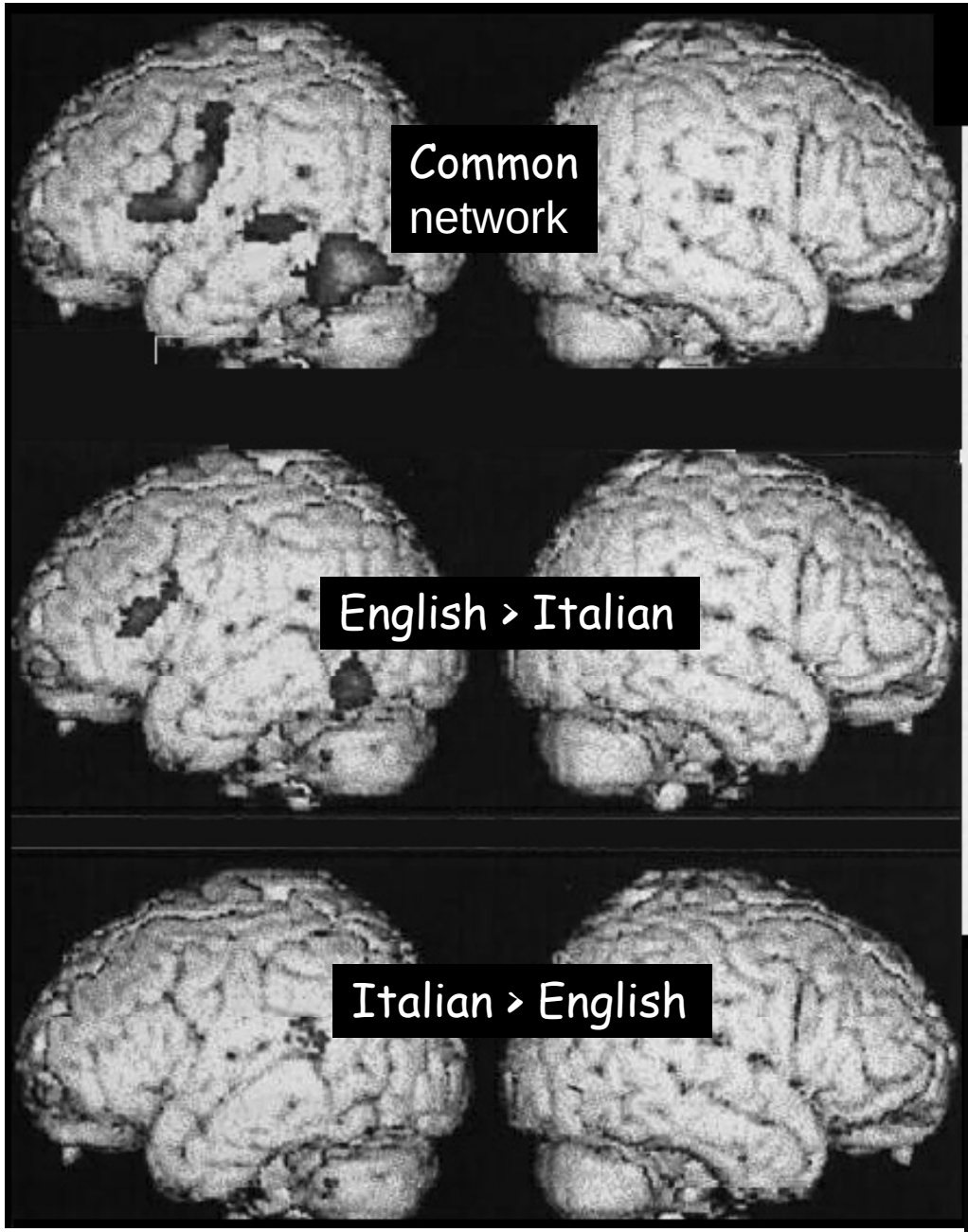
illiterates

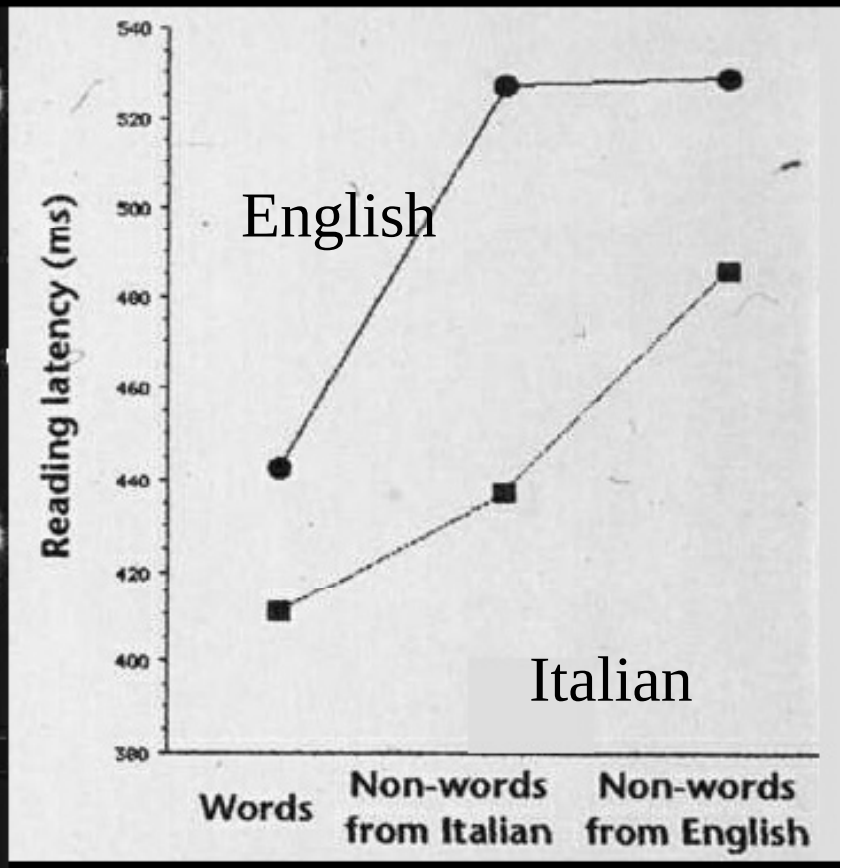


Castro-Caldas et al, 1998

culture

Can each of the many human languages be able to impact the brain circuitry subserving reading processes, depending on its specific features ?





opaque versus transparent phono/orthographic correspondences
Paulesu et al., 1999

nebucatnezar

nabuchodonosor

nebucatnezar

‘indirect’, sub-lexical route

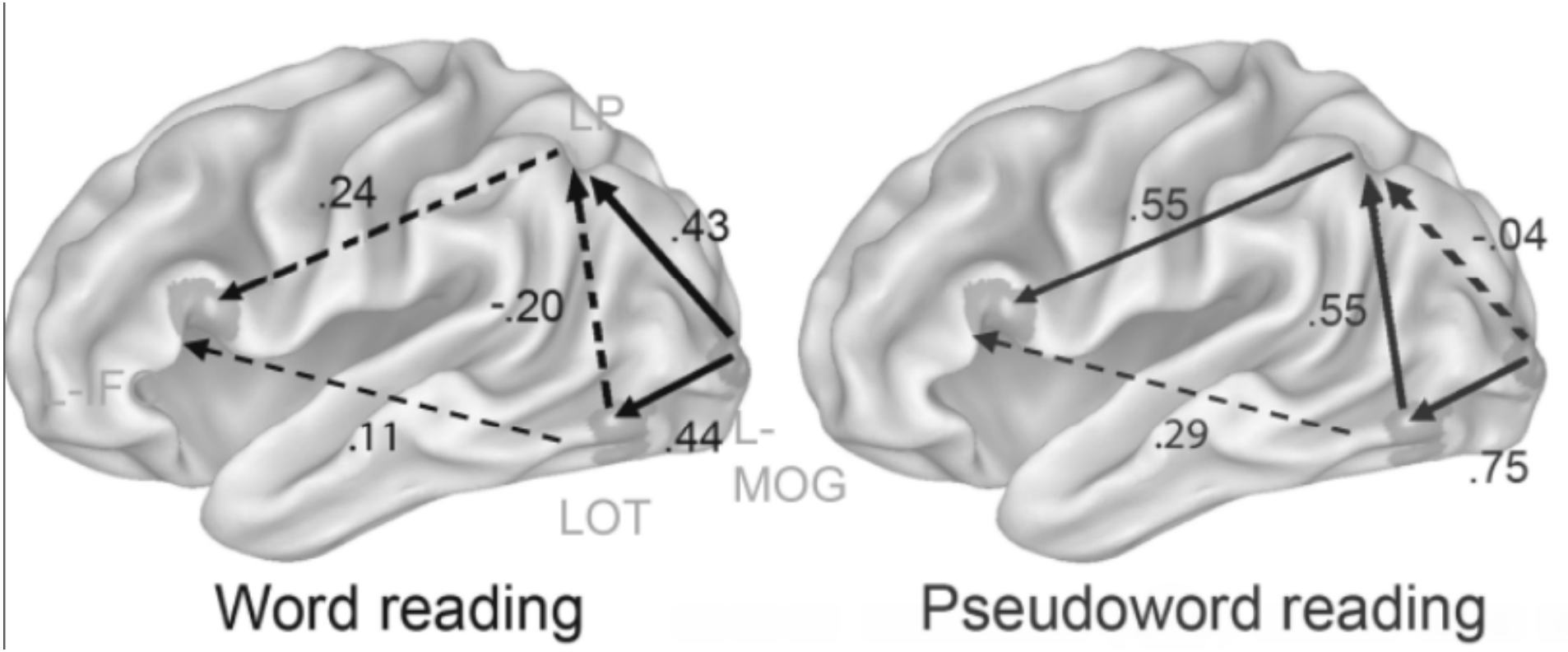
nabuchodonosor

‘direct’ lexical route

dual-route model for reading and writing

Effective connectivity analysis

Lévy et al.
PlosONE
2009

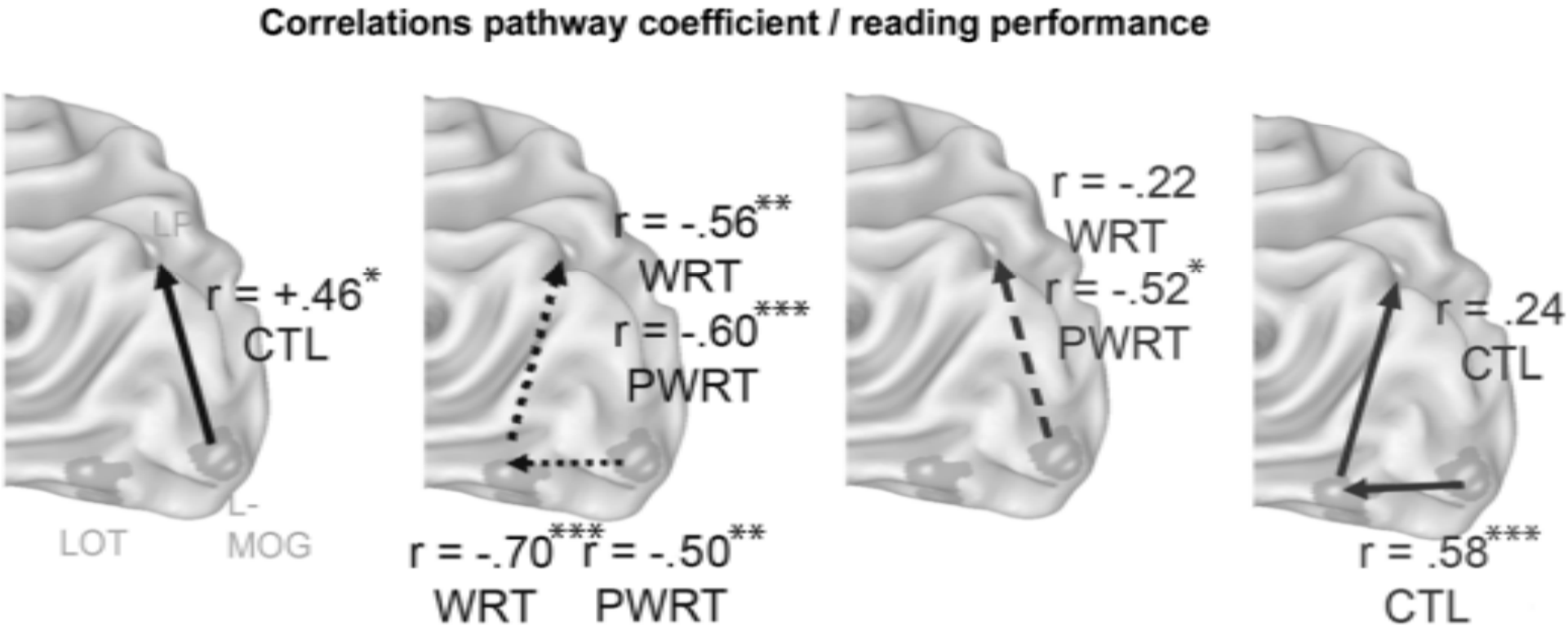


Nabucco

nebucatnezar

Effective connectivity analysis

Lévy et al.
PlosONE
2009

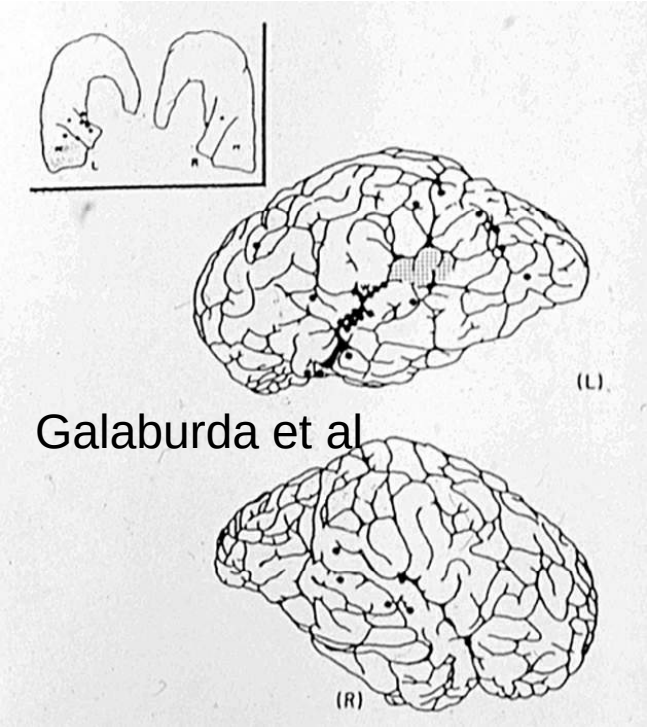


Nabucco nebucatnezar

the paradox of developmental dyslexia: a dysfunction of a culture-based ability with a biological origin :

While reading and writing only develop with explicit teaching, the specific impairment of learning to read and write (in seemingly healthy children) is attributable to specific biological disorders of brain functions.

Developmental dyslexia

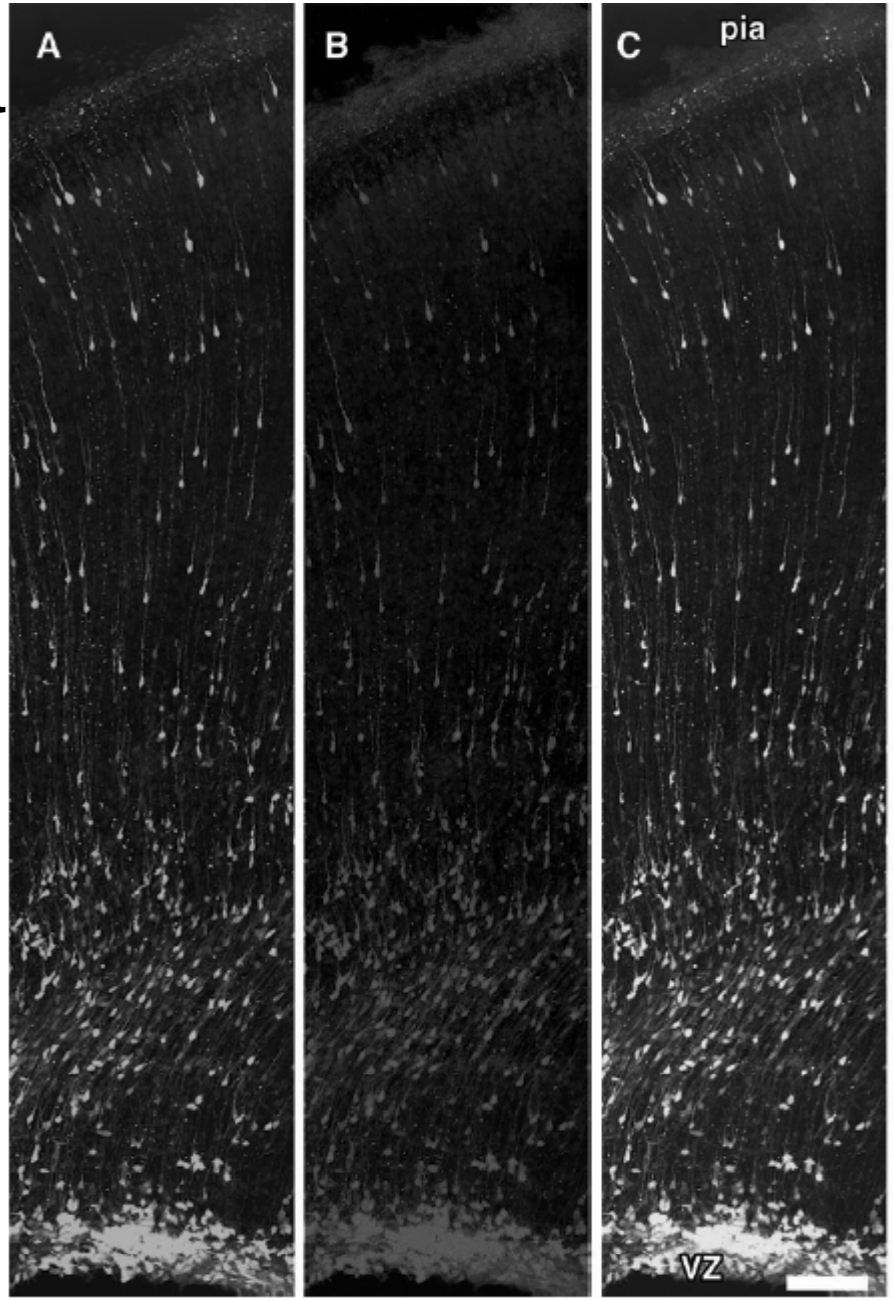


Galaburda et al

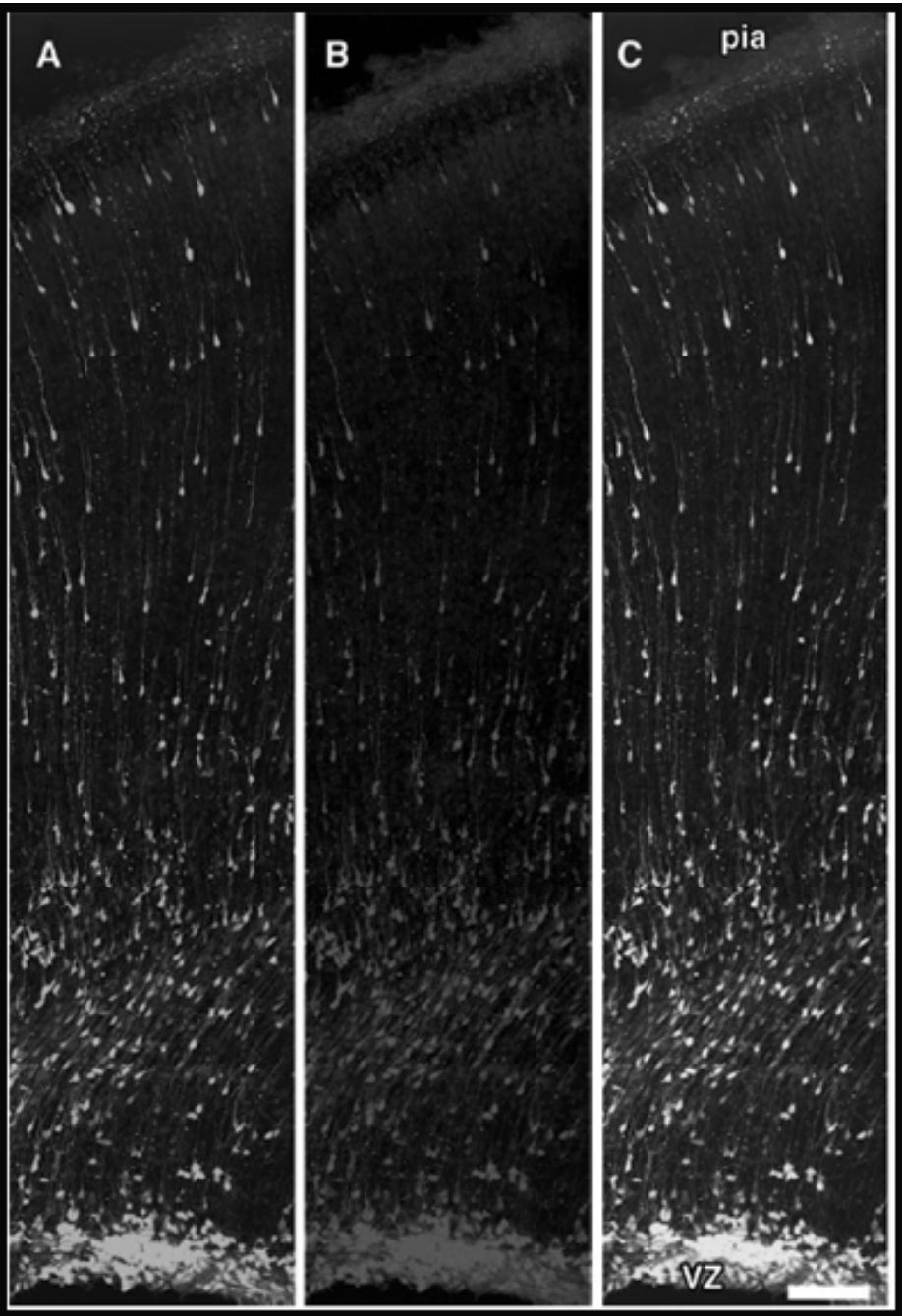
persistent and unexpected difficulties for automatizing reading and spelling

suspected multiple genetic factors

different phenotypes but involve
- slow reading
- poor phonological awareness
- poor spelling

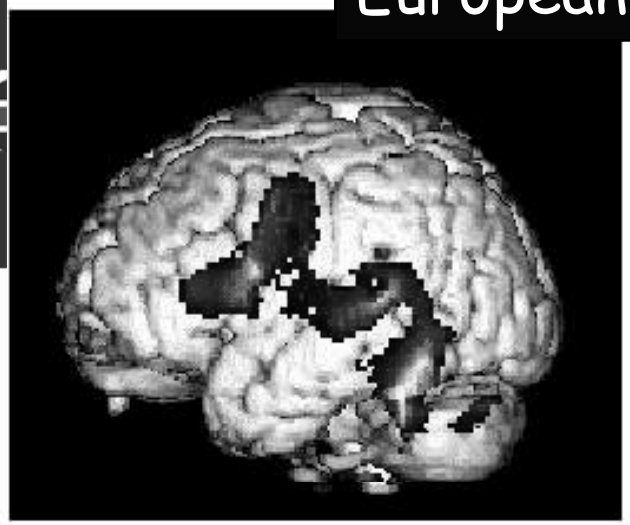


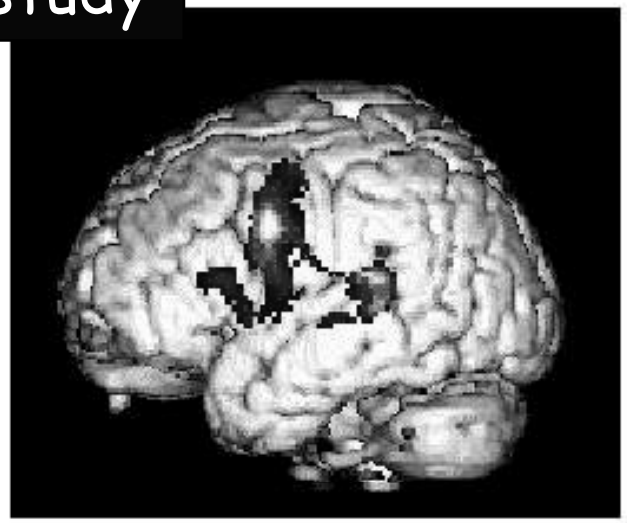
Rosen et al., Cerebral Cortex, 2007



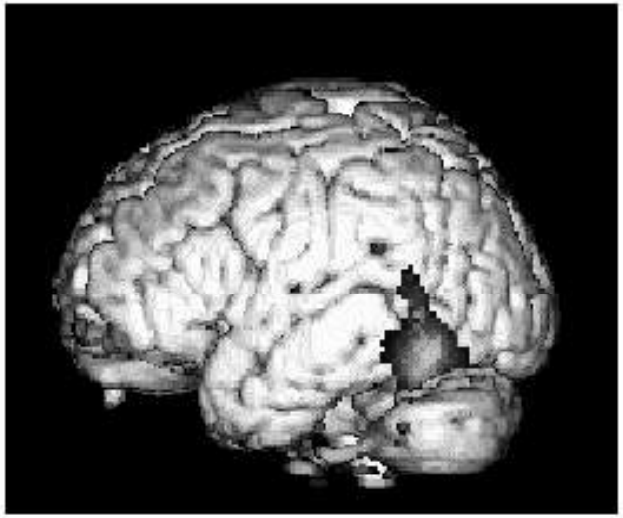
Rosen et al., Cerebral Cortex, 2007

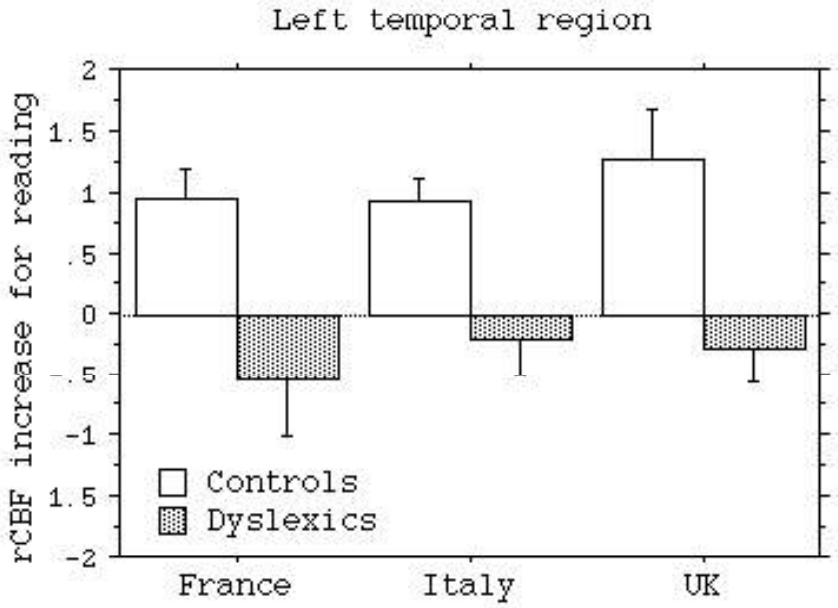
European dyslexia study



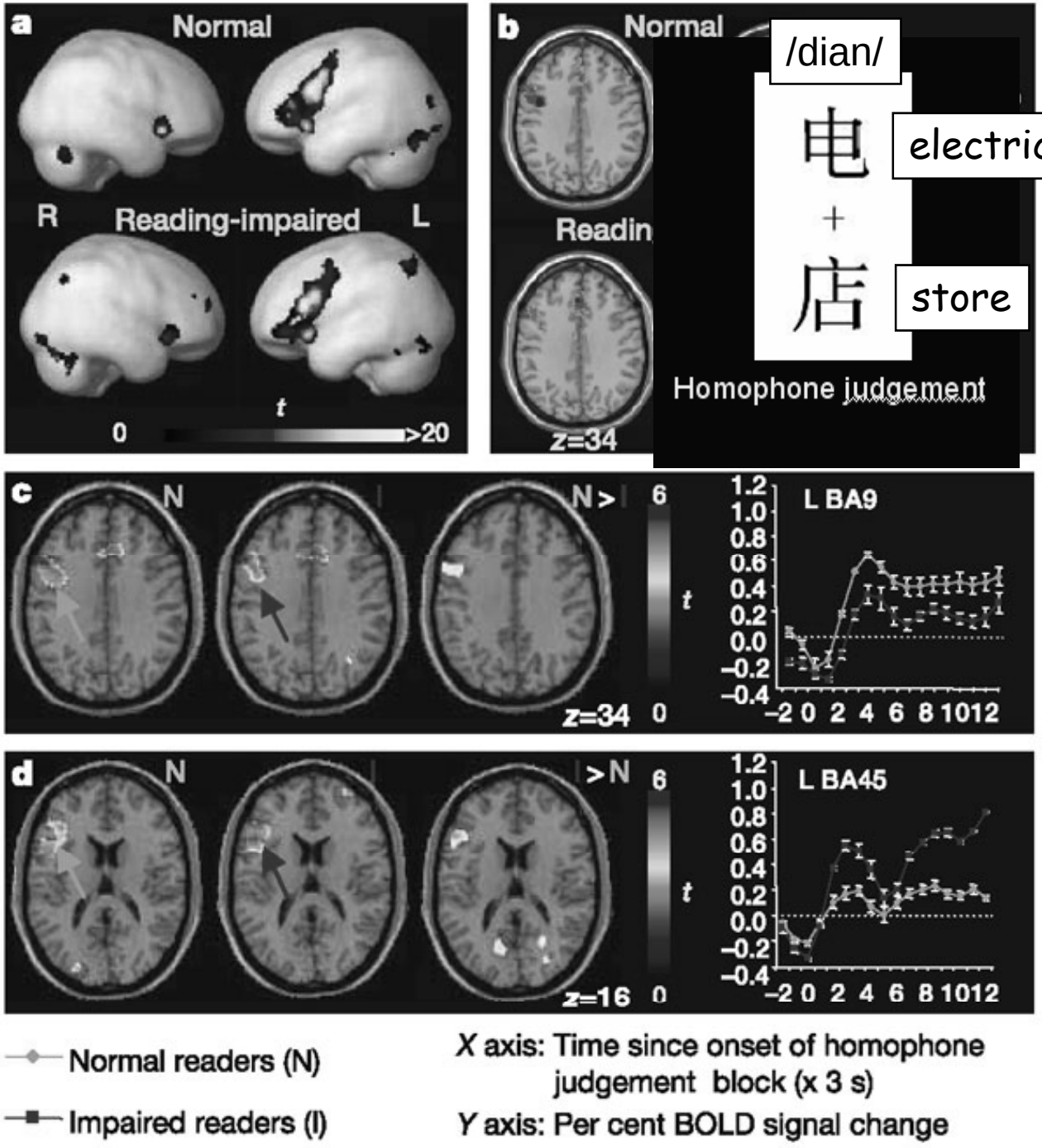


Word reading in dyslexics relative to controls





Paulesu et al., 2001



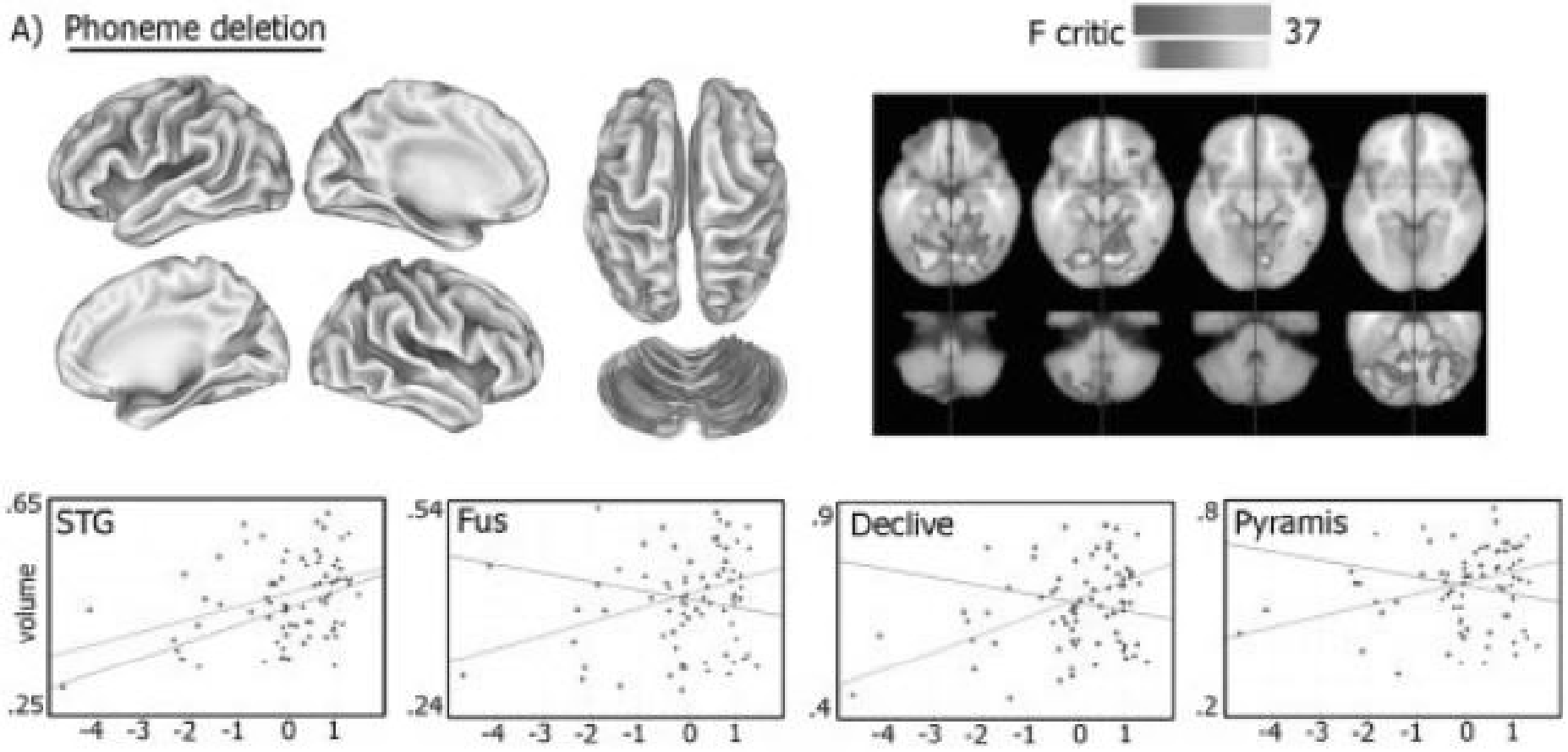
culture

Impact of ideographic Chinese Mandarin

might reading depend on motor codes used for writing ?

Siok et al., 2004

performance on phoneme deletion modulates gray matter volumes in cerebral and cerebellar regions, according to an opposite pattern in control vs dyslexic readers



Effects also observed for irregular word spellig and pseudoword reading tasks

Pernet et al., Human Brain Mapping, 2009

the writing brain

Phedre **(Plato)**

Plato mentioned the Egyptian legend of Thot as the divine entity that revealed to Humans the secrets of writing, the sources of Science and any wisdom or knowledge.

He also makes *Socrates* criticizing the use of handwriting as an impoverishment of human verbal memory that should rather be constantly exerted and maintained by oral training to discourse and dialog skills

Verba volant, scripta manent

Written language and memory

- verbal human memory got materialized thanks writing
(re Socrates in *Phedre*)
- reciprocally, considering subject's cognition,
several memory components, specifically related to language,
make it possible that written language is produced.
-These memory components can be sub-divided in two types
    - one relates to abstract orthographic entities
    - the other relates to specialized motor skills (e.g. piano playing

the crucial specificity of handwriting lies in
the interface between these two types of memory

What are the brain correlates ?

Sigmund Exner

1881 . 1376

UNTERSUCHUNGEN

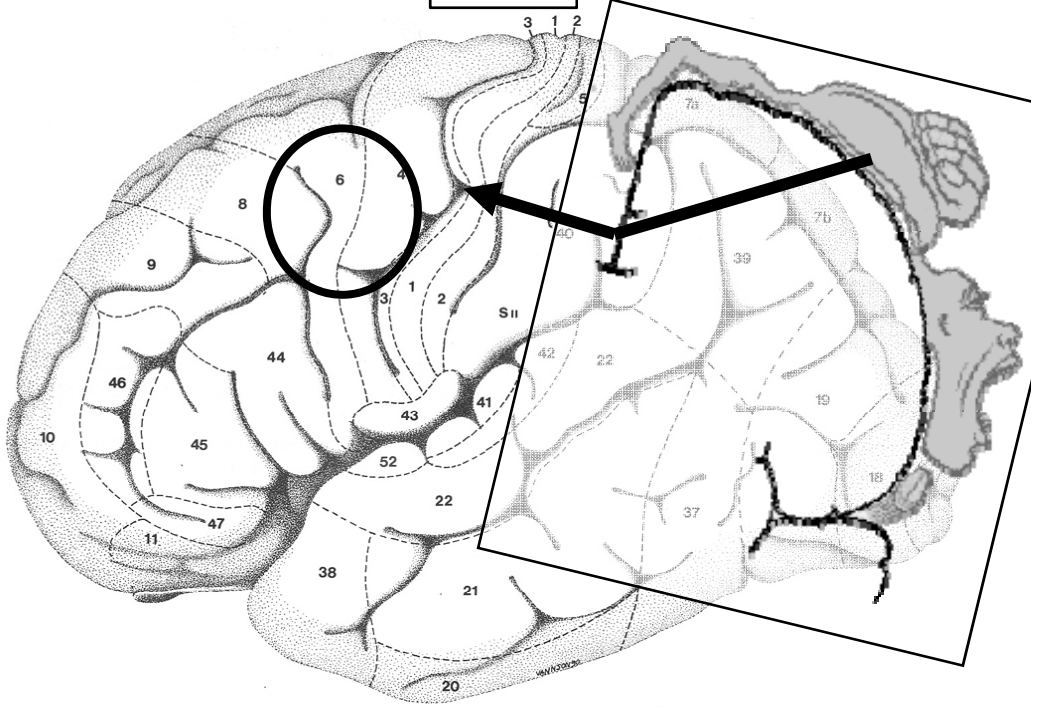
ÜBER DIE

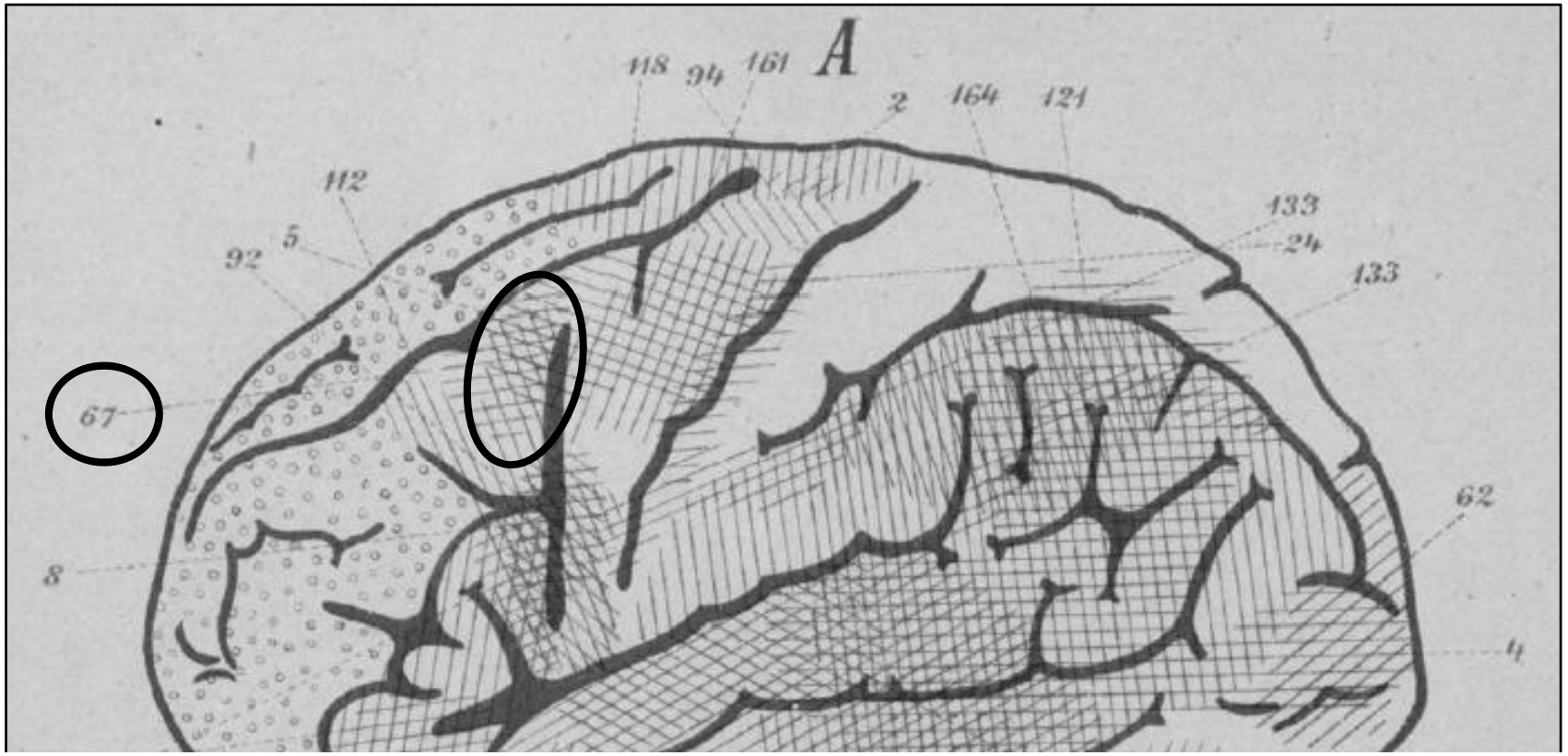
LOCALISATION DER FUNCTIONEN

IN DER

GROSSHIRNRINDE DES MENSCHEN.

1881





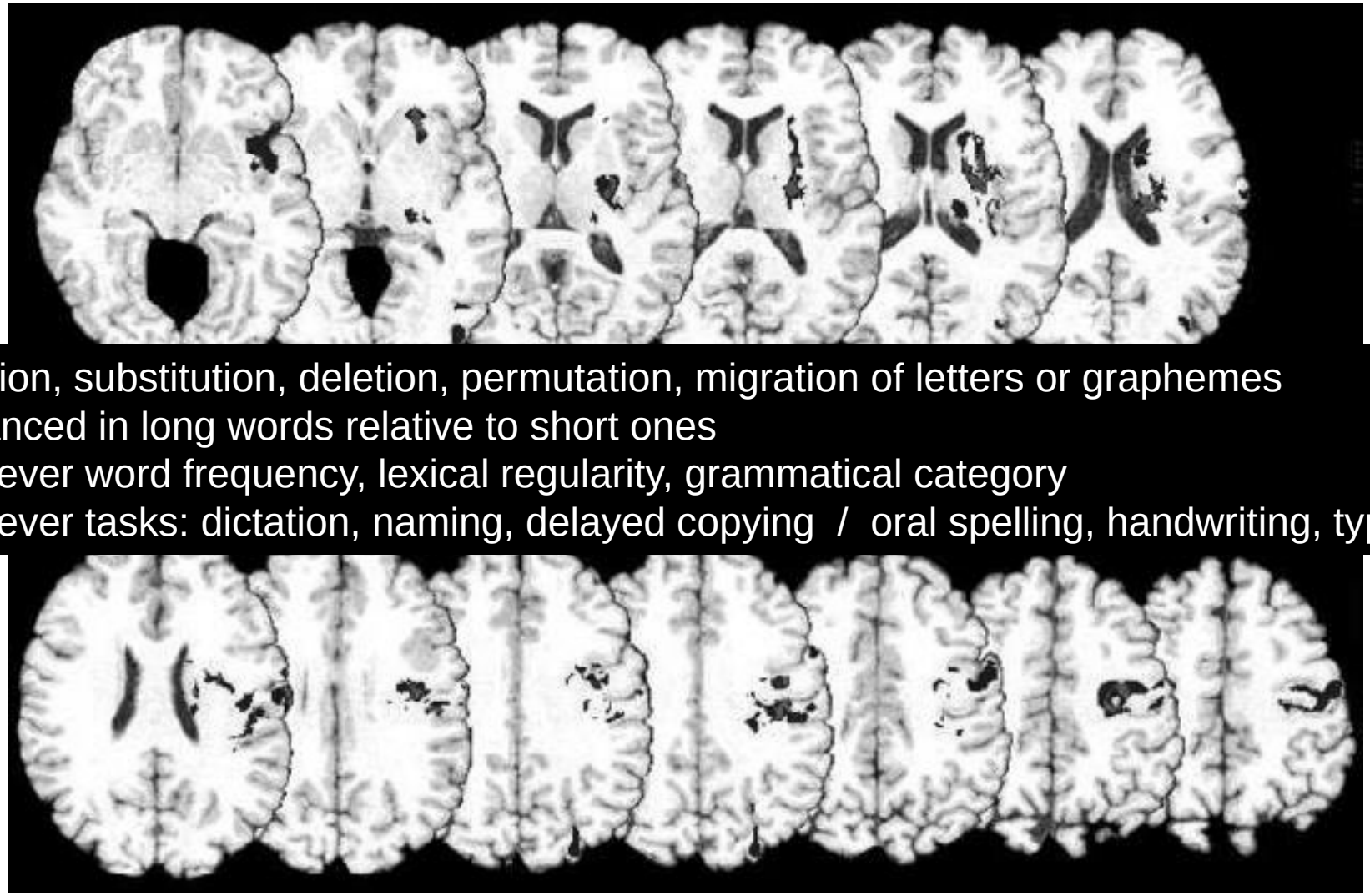
p.·103,·description·of·Case·#67¶

Mild·palsy·of·right-sided·face·and·upper·limb.·Aphasia.·At·the·beginning,·the·latter·was·accompanied·by·word·blindness;·then·word·comprehension·recovered·while·aphasia·and·agraphia·persisted.·Lastly·these·signs·also·disappeared.·¶

Haemorrhage·of·the·size·of·an·almond·surrounded·by·a·halo·of·0.5·cm·width,·in·which·the·cortex·was·also·destroyed.·The·lesion·is·located·in·the·gyrus·frontalis·medialis·where·it·touches·the·gyrus·centralis·anterior.·Drawing·in·Table·IX·A,·B¶

S. Exner, 1881, figure VIIA

lesion anatomy of the graphemic buffer syndrome

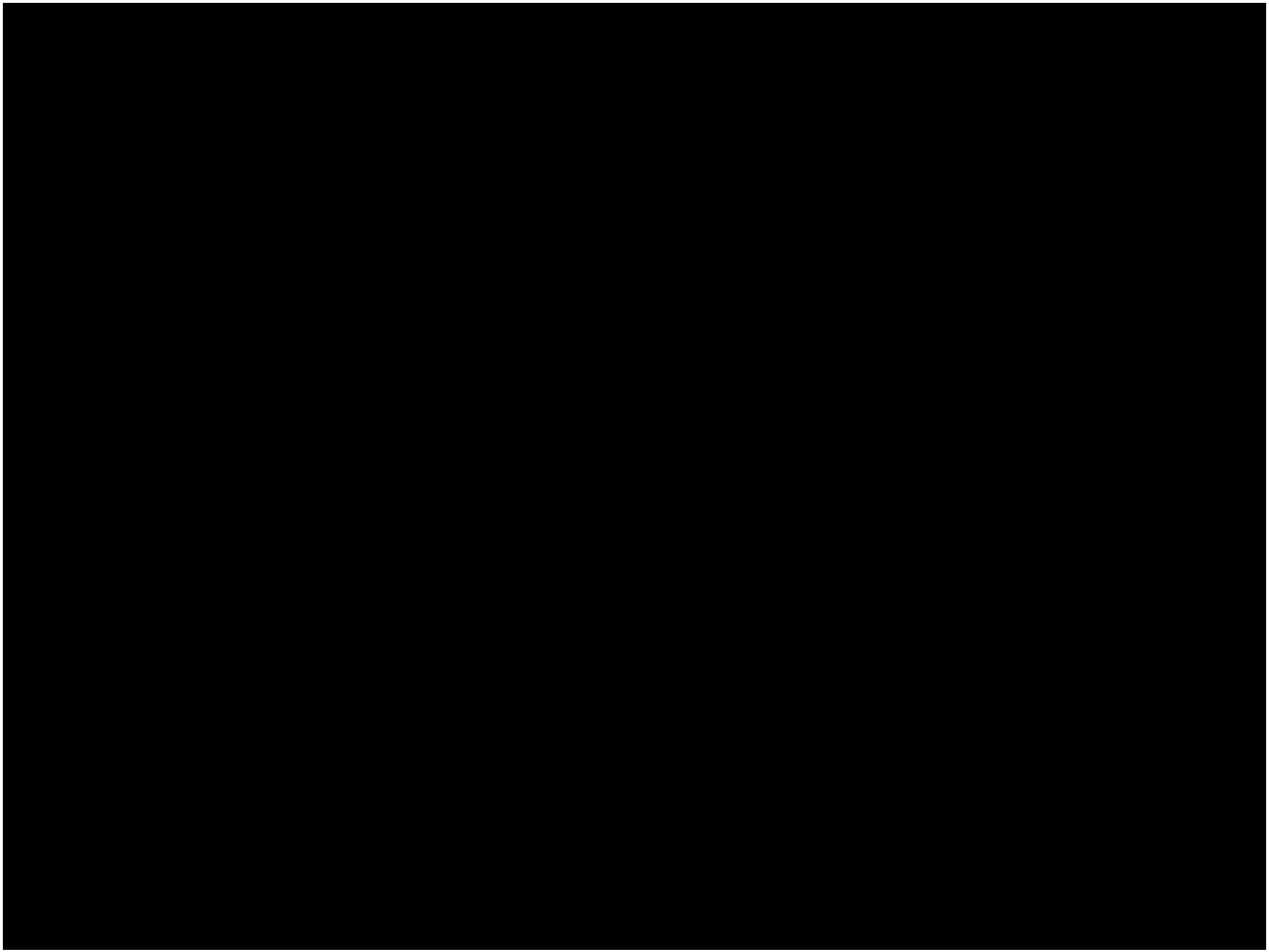


addition, substitution, deletion, permutation, migration of letters or graphemes
enhanced in long words relative to short ones
whatever word frequency, lexical regularity, grammatical category
whatever tasks: dictation, naming, delayed copying / oral spelling, handwriting, typing

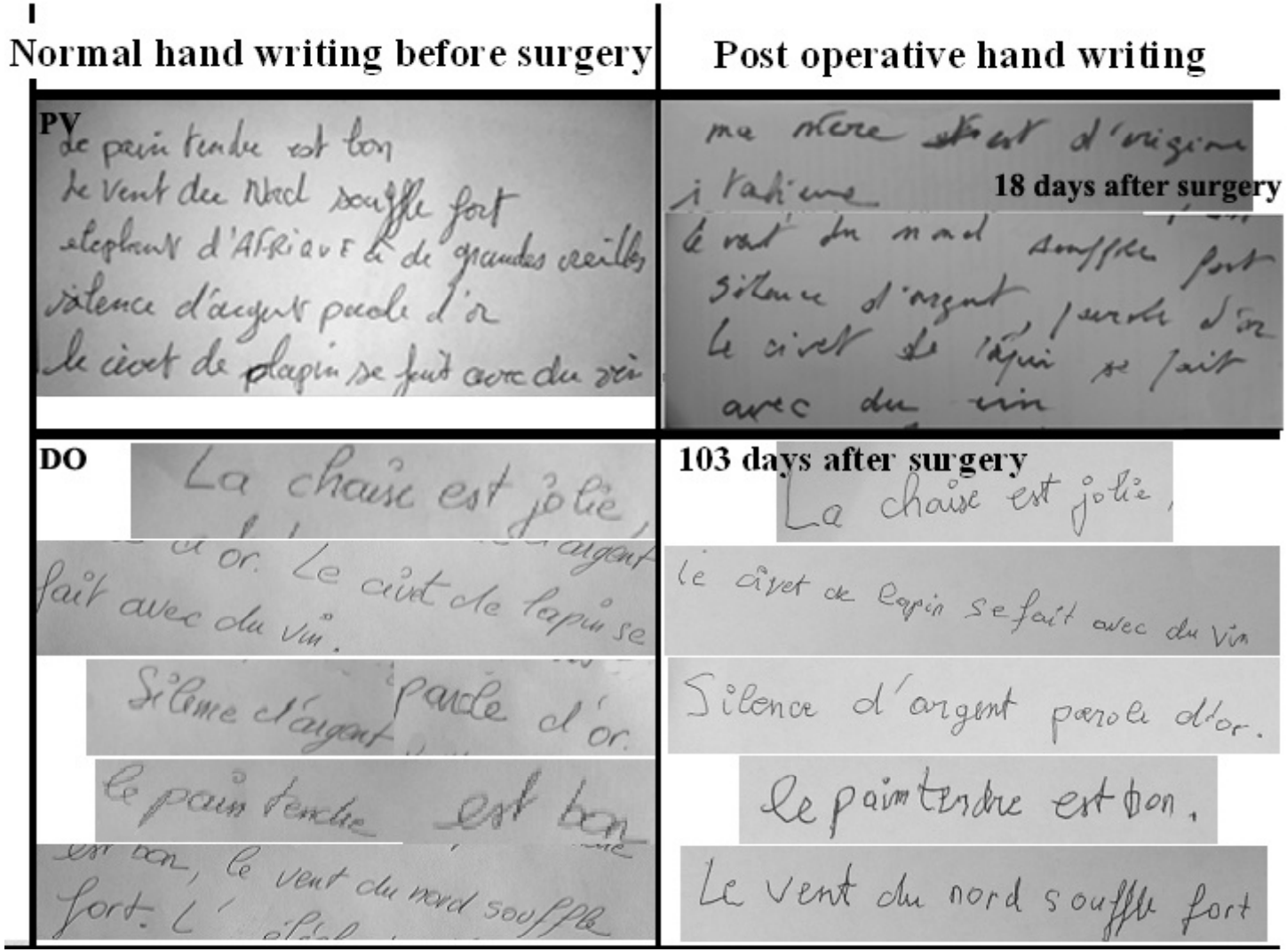
Cloutman et al., 2009

mapping of language functions during neurosurgery in awakened patients

direct electrical cortical stimulation: functional inactivation of discrete portions of association cortex



dysgraphia in 2 patients in whom a partial resection of the writing-related cortex was performed as it involved tumor tissue



fMRI experiment in 12 right-handed and 12 left-handed normal participants

word dictation tasks (+ other handwriting tasks)

performed with the preferred and non-preferred hand

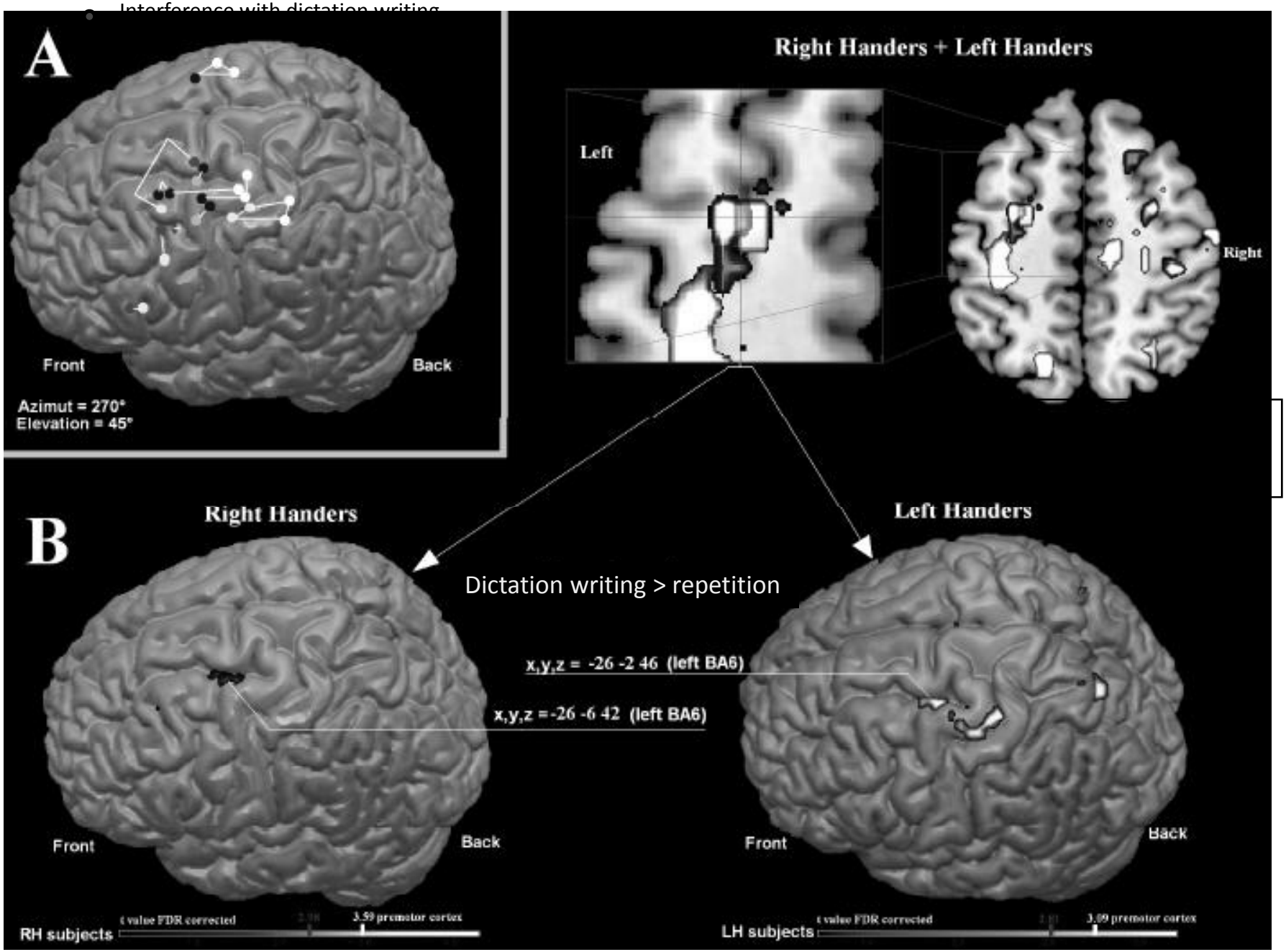
- control tasks :

aloud repetition of the same words

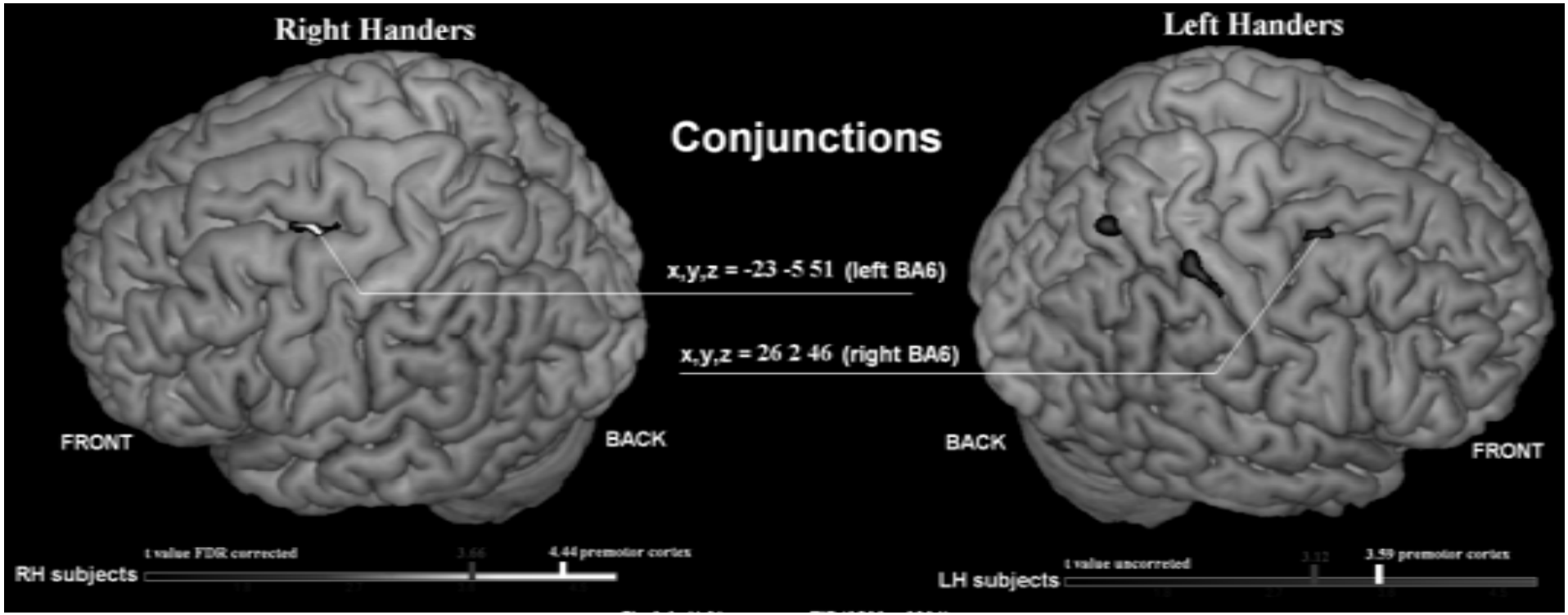
aloud repetition of meaningless syllable

circle tracing

- Interference with dictation writing



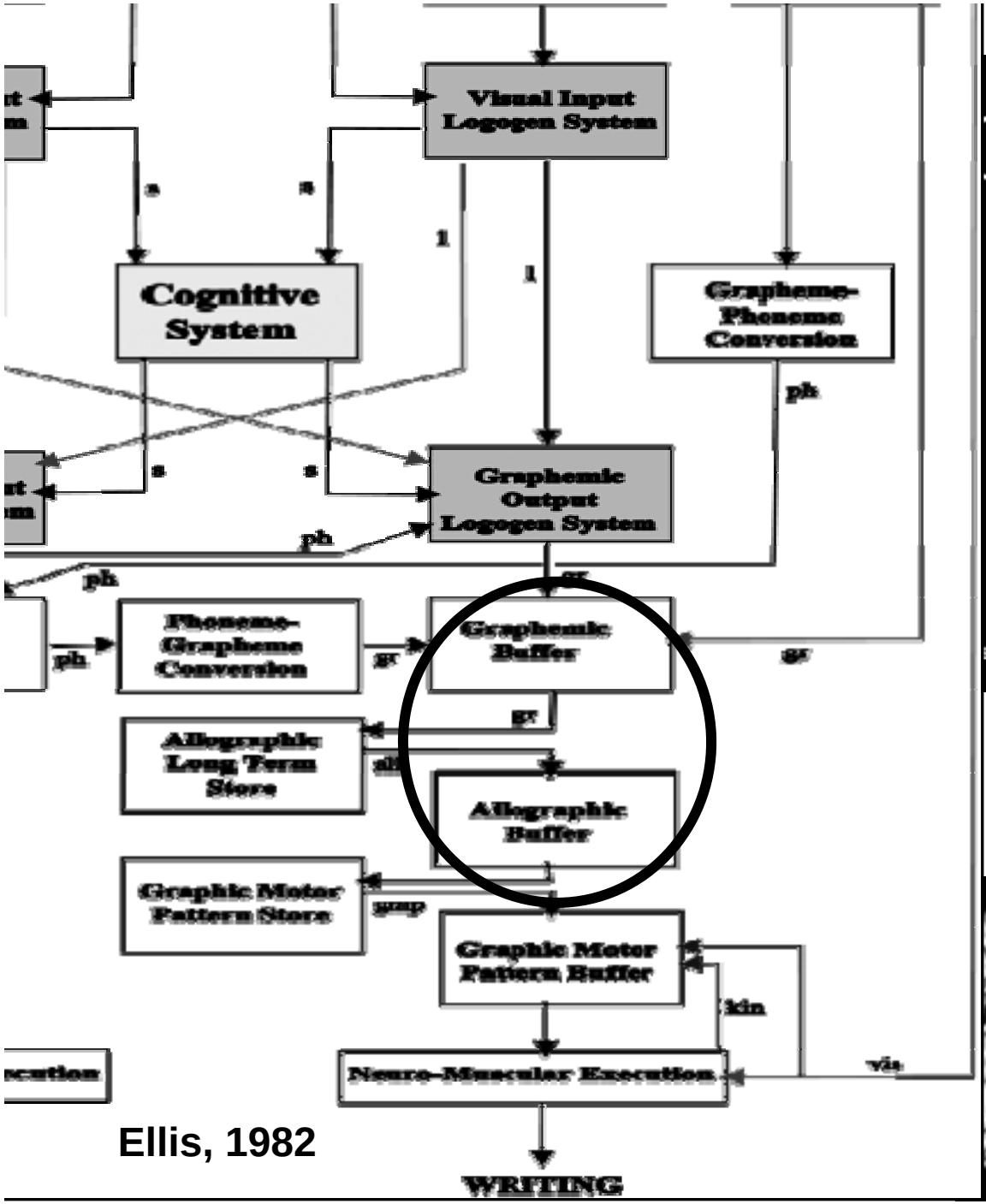
Writing with the preferred hand & with the non-preferred one



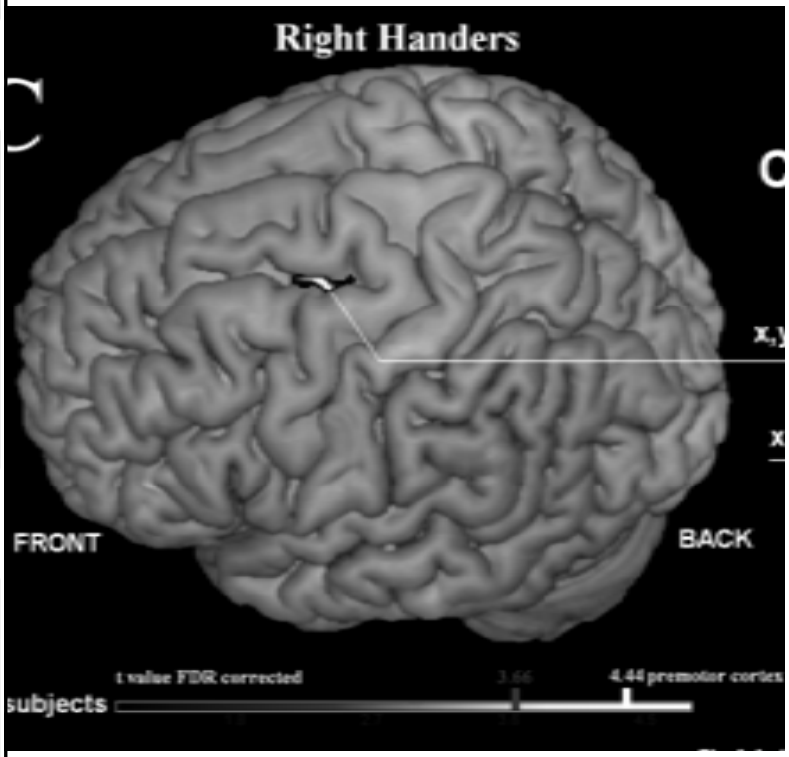
Roux et al., Annals of Neurology 2009

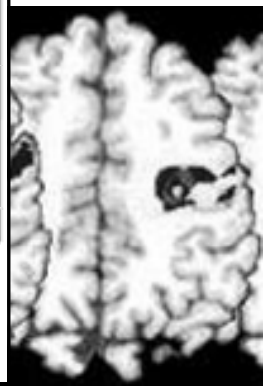
Functional significance in psycholinguistics terms ?

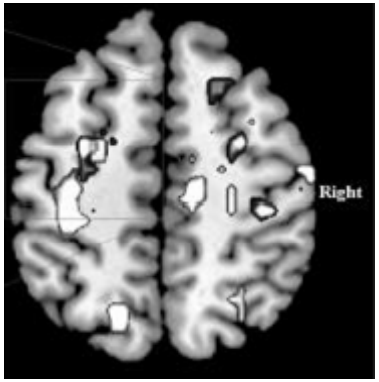
Word dictation - against repeatiing aloud same words
- excluding areas relating to « simple » graphic gesture (circle drawing on command)


Visual Input Logogen System
Cognitive System
Grapheme-Phoneme Conversion
Graphemic Output Logogen System
Phoneme-Grapheme Conversion
Graphemic Buffer
Allographic Long Term Store
Allographic Buffer
Graphic Motor Pattern Store
Graphic Motor Pattern Buffer
Neuro-Muscular Execution
WRITING
s
l
ph
gf
kin
vis

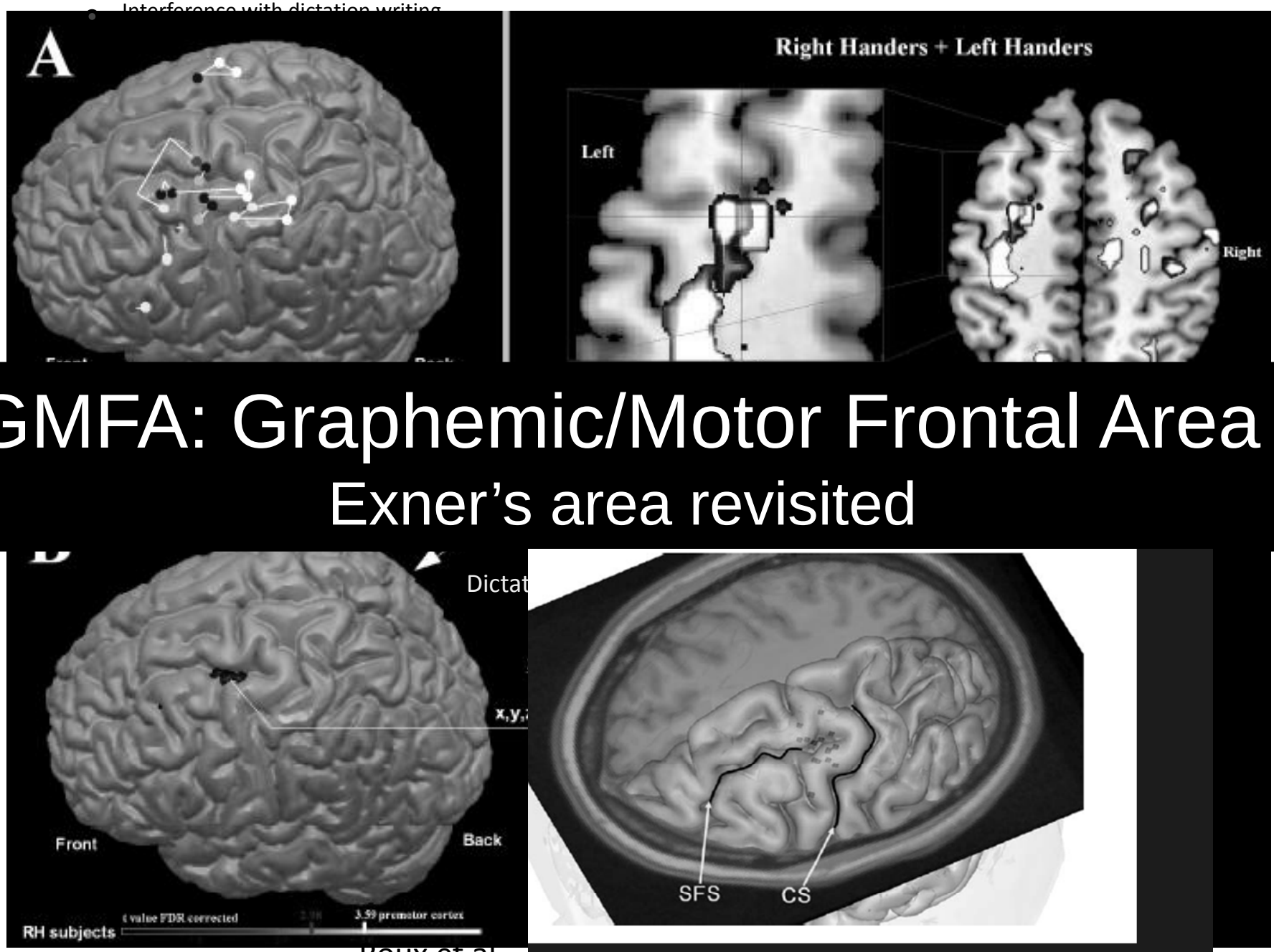
Ellis, 1982


Right Handers
FRONT
BACK
t value FDR corrected
4.44 premotor cortex
subjects




Right

- Interference with dictation writing



GMFA: Graphemic/Motor Frontal Area

Exner's area revisited

Dictat

Roux et al.,

Written naming (Sugihara et al., 2006)

future directions for the neuroscience of writing

- Effect of handedness
- Why is the GMFA bilateral ? Re: information traffic in the corpus callosum
- « where » is the orthographic lexicon ?
- Connectivity studies to reveal much more about the functional relationships between a number of other related areas including segregation between lexical and sublexical orthographic processing
- brain correlates of computerized writing modalities (keyboards, mobile phones, etc …)
- Spelling and writing disorders are induced by a variety of brain diseases,

  either developmental (dyslexia), focal (aphasia), or degenerative (Alzheimer, Parkinson, …)

  and are worth studying using neuroimaging,

conclusions ? Outstanding questions (1)

cognitive neuroscience provides some hints on the physiology of language; the contributions of individual-based, biological mechanisms (« nature ») and of social-based modulations (« culture ») are intimately intricated;

much can be learned from primate studies: e.g. metacognition: how close vs different from humans ? (Premack, *PNAS*, 2007)

* « nature »

- how does language network interact with "background" brain systems : « what-where », « mirror neurons », embodiment of semantics ?

- what are the genetic and biological mechanisms governing the spontaneous development of spoken language ?

conclusions ? Outstanding questions (2)

* multiple "nature /culture" interactions

- physiology of inter-subject communication and social cognition (verbal and non-verbal) ?

- how can specific languages (e.g. written systems) influence the brain substrates of language processing ?

- how far does music overlap with language in terms of physiological substrates?

- in appropriate biological conditions, what are the mechanisms of the early adaptation to mother-tongue (re: commitment of neural networks to mother-tongue system, Khul, 2004) ?

- physiology of second language learning, in pre-school children versus once reading has been acquired, ? automatization ?