Brain lateralization and the emergence of language

Nathalie TZOURIO-MAZOYER

Atomic Energy Commission (CEA)
Groupe d’Imagerie Neurofonctionnelle (GIN)
Neuroimaging platform Cyceron Caen
CINAPS  UMR 6232 CEA CNRS
tzourio@cyceron.fr
Hemispheric specialization is a brain functioning organizational principle that governs in particular the large scale neural support of language.

According to Tim Crow HS is at the origin of human speciation and language, and psychosis is “the price to pay for language”.

Animal studies have shown that HS is not unique to humans (Valortigara, Hopkins) but its expression is at its utmost in the human species.
Definition of hemispheric dominance for language

Relationships between left-hemisphere dominance for language and right-handedness

Hemispheric organization for language in right-handers

Left-handedness and language production’s areas variability

Brain volume and anatomical asymmetry of auditory areas explains the variability of hemispheric specialization of speech areas

Conclusion: perception and action pole of language hemispheric lateralization is related to different factors
LH specialization or dominance for language

Phrenologists brain functionally and structurally symmetrical

Mr Leborgne (1861)
Paul Broca (1824-1880)

Carl Wernicke (1848-1905)
LH specialization or dominance for language

Sentence comprehension deficits
Wernicke’s aphasia
Perception pole  Dronkers 2004

Speech production deficits
Broca’s aphasia
Action pole  Borovsky 2007

Mesulam 1998,
Fuster 1998
Language lateralization and handedness

Language and manual preference are the most asymmetrical behavioral and brain functions in humans.

LH hosts both language and control of the right hand.

Same proportion of left-handers (9%; 22% right negative hand) since Paleolithic (-10 000 -30 000 y)

_ Faurie 2003_

Aphasiology, WADA, cortical stimulation: 92 à 99% of right-handers have a left hemisphere dominant for language (_Rasmussen, Damasio, Ojemann…_)
Language lateralization and handedness

Strength of hand and language lateralization link

Plasticity of hand-language lateralization
- Individuals that suffered form a LH lesion before 1 year old shift both language and handedness to the RH (Woods 1988)
- Individuals with right plexus brachial injury at birth have a left-to-right shift in language production areas increasing with the severity of the hand usage dysfunction (Auer 2009)
- Training of the non-dominant hand for complex movements improve the recovery form non fluent aphasia and is associated with a increase rightward asymmetry during production tasks (Crosson 2005)

Linguistic link
- Activation of left premotor areas by tools naming or action verb processing, somatotopically organized (Buccino 2001)
- Right-hand reaching movement are modified by lexical task involving action verbs (Boulenger 2006)
- Side of hand premotor areas involved in lexical decision on manual action words follows handedness (Willems 2009)
LH dominance for language in right-handers

Meta-analysis: 129 studies, 1000 healthy right-handers

PET and fMRI, results reported in stereotactic coordinates (x, y, z)

Peaks in precentral, F2, F3, T1, T2, T3, insula, fusiform, AG, & SMG

Classification of LH and RH peaks into 3 components:

- **Phonological**: human voice, syllables…
- **Semantic**: words, images categorization..
- **Sentence/text**

Selection of contrasts with high-level reference

Talairach, 1967 & Fox 1988
LH specialization in right-handers

Phonological tasks

Semantic tasks

Sentence/text processing

LH: 728 peaks

RH: 218 peaks
LH dominance for language in right-handers

Most LH peaks are **unilateral**

L Unilateral 574 (78.9%)

Most RH peaks are **bilateral**

R Unilateral 73

For each language component, classification of:

- **bilateral peaks**: one RH peak having a LH peak of the same study and same contrast and located within 20 mm Euclidian distance (ED) of its symmetrical position

- **unilateral (right or left) peaks**: RH or LH peak having no symmetric peak located within 20 mm of ED

LH dominance for language in right-handers: development

Leftward lateralization linearly increases during development.

Cross-sectional study of 20 subjects 9-20 years, rhyming and synonym tasks

Longitudinal study of verb generation in 29 children aged 5-11 years followed during 5 years once a year

Everts 2006

Szaflarski 2006
In right-handers the intimate relationship between hand and language lateralization in the brain is one of the element of the motor and gestural theories on the evolution of language:
- Brain organization for complex movements as the evolutionary support of language areas (Lieberman, 2002)
- Gestural origin of speech (Corballis, Arbib)

How does handedness interact with the neural support of language? How varies the hemispheric representation of language areas with handedness?
Handedness and language specialization

HEMISPHERIC LEVEL

Aphasiology
• 30%-60% of LH lesioned left-handers patients are aphasics after both LH and RH lesions (Loring 1990), they show ambilaterality (Hécaen 1971)
• Patterns of lateralization: L15%, R15%, ambilateral 70 % (Satz 1979)

WADA
• 15 à 19% of non right-handers epileptics are ambilateral or rightward dominant (Wada 1960).
• Incidence of atypical language dominance varies with strength of handedness: 9% in strong right-handers, 46% in ambidextrous, 69% in strong left-handers (Isaacs 2006)

fCTD of word generation
4% of atypical lateralization in strong right-handers, 15% in ambidextrous, 27% in strong left-handers (Knecht 2000)

=> The stronger the right-handedness the stronger the language-hand lateralization link. Language-hand lateralization link is loose in left-handers.
Regional level in healthy subjects: functional imaging

Inter-individual variability of speech listening in left-handers

PET

Rest  Text  Text - Rest

Tzourio 1998
Handedness and language specialization

⇒ lateralization of production and comprehension is lower in left-handers
⇒ in frontal areas leftward recruitment increases with right-handedness during language production task.
- Crossed aphasia in right-handers *(Alexander and Annett, 1996; Coppens et al., 2002; Hindson et al., 1984)*
- Healthy right-handed individuals with mirrored recruitment of right IFG during verb generation

**Crivello, 1994**
Handedness does not explain all

- Epileptic patients show dissociation on Wada testing (4/490) \( (\text{Lee 2008}) \)

- Healthy subjects can display dissociation of lateralization of the perception and comprehension poles \( (\text{Tzourio-Mazoyer 2004}) \)

**Right-handed man, ES=100**

**Left-handed man, ES=-60**

Production of sentences  |  Listening to sentences
Perception side

Previc proposed a general theory on the prenatal origin of HS (1991):

Position of the fetus during third trimester of fetal life results in an asymmetrical craniofacial development and an aural lateralization favoring the right ear:

- 60% of fetus confined to a leftward fetal position, right ear facing out
- Greater likelihood of opposed handedness in twins
- Decrease lateralization in preterm infants

Different specialization of the right and the left hemisphere auditory cortices (Zatorre 2005, Poeppel 2003).

- Right is specialized for tonal processing
- Left for temporal processing necessary to perceive language sounds

The auditory associative cortex of the planum temporale is the only cortex showing a large macroscopical leftward asymmetry
Planum temporale: largest leftward brain asymmetry

Leftward asymmetry (100 individuals)

Probabilistic map

Auditory associative area

Geschwind 1968
Westbury 1999
Galaburda 1978
Related to a global anatomical asymmetry of the brain

“Petalia” & “Yakovlevian torque”

RH temporal sulci moved forward

Toga, 2003

Petalia displayed in 82% of modern hominids 25% of great apes

Blanton 2001
Related to a global anatomical asymmetry of the brain

Michel Habib
PT asymmetry appears early in development

34ème gestational week along with primary sulci appearance
Identical asymmetry in adults and term newborns

Chi, Arch Neurol 1977

Van Essen, J Neurosci, 2010
• 14 male volunteers, 5 left-handers,
• PET during speech listening
• the larger their left PT the larger their activation in the left temporal gyrus

Asymmetry of auditory areas, that are established at birth, are related to the leftward asymmetry of speech comprehension areas

Tzourio N, 1998
PT asymmetry handedness and brain volume

Handedness does not influence the width of the left PT or its asymmetry (274 volunteers, 80 left-handers)

Brain volume (BV) do: when BV increase, left PT surface and its asymmetry increase

Brain volume increase is one of the major feature of evolution, it is concurrent to the emergence of language  

_Schoenemann, 2006_
When a high speed of processing is needed, hemispheres are more efficient when they work separately because of the increase to the transfer time through the CC in bulky brains.

2 symmetrical « cerebral networks », linked by connections (simulating the corpus callosum) with different speed.

Performances of the networks at a recognition task before and after «callosotomy».

- at low speed no difference between the 2 networks
- at high speed the network with slow inter-hemispheric connections is more efficient ⇒ intra-hemispheric processing when temporal speed is needed (Ringo 1994)

Increasing BV conducts to clusterization of functional networks

When a high speed of processing is needed, hemispheres are more efficient when they work separately because of the increase to the transfer time through the CC in bulky brains.
BV, inter-hemispheric transfer & language lateralization

Through evolution the larger the brain the smaller the relative size of the corpus callosum connecting the two hemispheres (Hopkins 2000).

In humans, the larger the brain the smaller the relative size of the corpus callosum (Jäncke, 1998).

Is BV related to functional lateralization of language areas?
Speech listening variability, BV, MP and L PT

20 volunteers, 8 left-handers, PET Hemispheric asymmetry CBF (L-R)
Multiple regression analysis

<table>
<thead>
<tr>
<th></th>
<th>Partials’ coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^2$</td>
<td></td>
</tr>
<tr>
<td>$LPT$</td>
<td>0.52</td>
</tr>
<tr>
<td>$MP$</td>
<td>0.48</td>
</tr>
<tr>
<td>$BV$</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Leftward asymmetry increases with large LPT surface, large BV and rightward MP

In the same subjects, during speech production, left frontal activations were related only to MP

⇒ The lateralization of the perceptive and action pole of language are influenced by factors that are partly different
⇒ It explains the observation of dissociations
According to Hécaen’s studies of aphasics left-handers, FS+ left-handers have the lowest language lateralization.

Healthy FS+ left-handers have lower lateralization during verb generation (Szaflarski 2002), with larger RH participation (Hund-Giorgadis 2002).

FS+ decreases the left PT surface area but not right PT, independently of handedness (Tzourio-Mazoyer 2010).

These results suggest at least partly independent mechanisms for the inheritance of hand and language lateralization.
Are BV, MP strength and FS (the fact of having a left-hander among close relatives) associated with differences in language functional lateralization?

- 49 right-handed volunteers fMRI Hemispheric asymmetry CBF (L-R)

Specific of language networks
Independent of handedness

_Tzourio-Mazoyer 2010, in revision_
Studies of healthy individuals with anatomo-functional imaging show that multiple factors influence the hemispheric asymmetries of language areas:
- Not only handedness but also its strength and FS
- Anatomical variables (BV, left PT size)

The inter-individual variability of the action and perception poles of language is explained by a different combination of factors:

1- Influences of BV and left PT surface on the posterior language areas support the hypothesis that perceptive constraints on the processing of speech sounds act on the development/evolution of hemispheric language organization.

2- Influence of handedness both on action and perception poles is compatible with the motor and gestural theories of the origin of language.
Special thanks to the GIN team

Emmanuel Mellet
Bernard Mazoyer
Laurent Petit
Gael Jobard
Laure Zago
Fabrice Crivello
Marc Joliot