

Language, speech, and cerebral asymmetry

Michael C. Corballis
University of Auckland

Historical overview

1. Handedness

- Right-handedness applies to all known cultures, as far back as the historical record takes us.
- This implies left-hemispheric dominance for skilled action
- Yet some 12% of the population is left-handed or ambidextrous

Pythagorean Table of Opposites (recorded by Aristotle)

LEFT	RIGHT
• The even	• The odd
• The unlimited	• The limited
• The many	• The one
• The female	• The male
• The curved	• The straight
• The dark	• The light
• The evil	• The good

2. Language and speech

- Left-hemispheric control of speech discovered by Broca in 1860s
- In 1870s, Wernicke discovers left-hemisphere dominance for comprehension
- Left hemisphere also dominant for sign language
- Yet some 12% of the population have bilateral or right-hemispheric language

19th Century Dual-Brain Story

LEFT BRAIN	RIGHT BRAIN
rational	<i>emotional</i>
sane	<i>insane</i>
civilized	<i>uncivilized</i>
masculine	<i>feminine</i>
European	<i>non-European</i>

Therapies include metallotherapy, hemi-hypnosis, use of magnets, etc, to “balance” the hemispheres

3. Right-hemisphere specializations

- Hemineglect reveals right-hemisphere dominance for attention
- Suggests left hemisphere controls attention to right side of space, and right hemisphere to BOTH sides of space.

4. Split-brain research

- Split-brain work in 1960s confirmed general left-brain dominance for language
- But also shows further right-hemispheric specializations
- These may include mental rotation, musical perception, holistic perception

20th Century Dual-Brain Story

LEFT BRAIN

reason
propositional
analytic
male
rule-bound
Western
civilized

RIGHT BRAIN

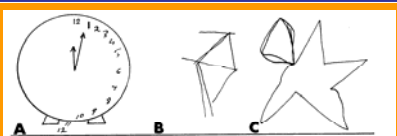
emotion
appositional
holistic
female
creative
Eastern
indigenous

Therapies include Superlearning, Neuro-Linguistic Programming, etc, to “release” the right hemisphere

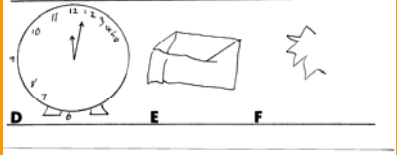
Some specific examples

EXAMPLES OF HEMINEGLECT

Left Neglect



Right Neglect



Note: Right neglect does occur, but is usually transient

ENVIRONMENT-CENTERED NEGLECT



Q: “Now will you draw this fence in for me?”
A: “Well, I will if you really want me to, but it will probably blow down in the next wind!”

—Ogden, J.A. (1985). *Brain & Cognition*, 4, 59-75.

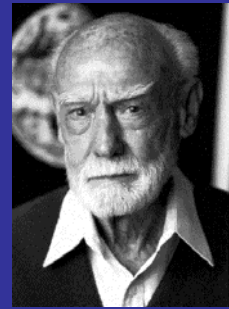
Split-brain research

Based on people who have undergone section of corpus callosum for relief of intractable epilepsy

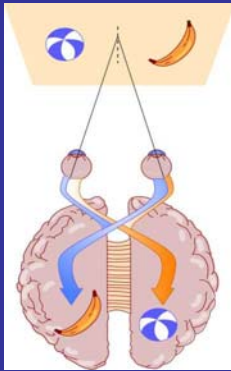
In this scan, arrows show intact anterior and posterior commissures following callosotomy



Roger W. Sperry

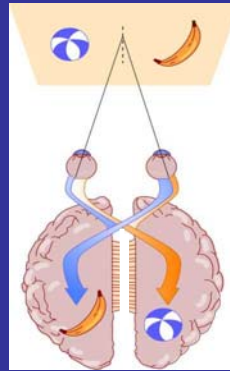


Nobel Prize, 1981, "for his discoveries concerning the functional specialization of the cerebral hemispheres"



The ball is projected to the right brain, the banana to the left.

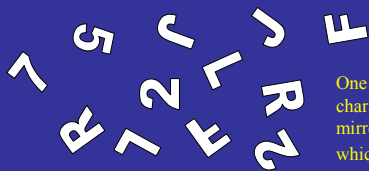
You need to flash the information quickly (less than 200 millisecc) so that fixation doesn't shift



If the brain is split, the ball remains isolated in the right hemisphere.

Since speech is in the left hemisphere, the patient cannot name the ball, but can easily name the banana

Mental rotation

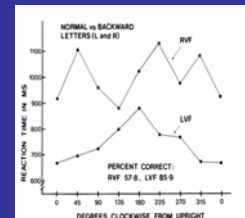
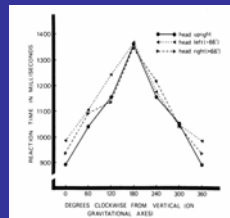


One of these characters is mirror-reversed. which one?

People are timed as they decide whether rotated letters like these are normal or backward

Mental rotation

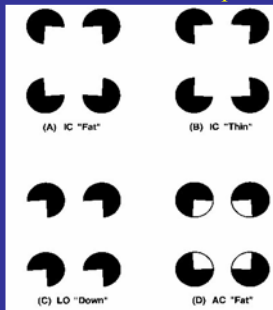
- RT plotted against orientation in normals
- RT plotted in a split-brained man (L.B.)



L.B.'s right hemisphere accomplishes the task, but the left cannot

—Corballis, M. C., & Sergeant, J. 1988. *Neuropsychologia*, 26, 13-26.

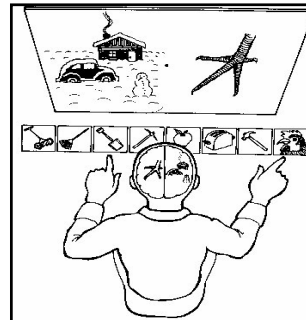
Another example of right-hemisphere advantage in the split brain



← Both hemispheres of the split brain equally adept at this

← Right-hemisphere advantage in this "window" version

Corballis, P.M. & Fendrich, R. *J. Cog. Neuro*, 11, 459-466.



Patient asked to point to object related to what he sees. Right brain chooses shovel, left brain chooses chicken.

When asked why he points to shovel, he says "to clean out the chicken shed!"

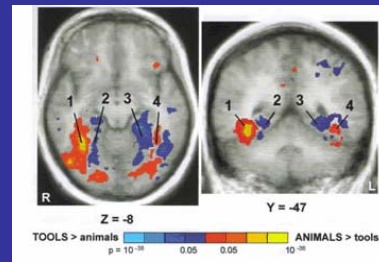
This has been taken to mean that the left brain is the **interpreter**

—Gazzaniga, M. S. (2000) *Brain*, 123, 1293-1326

Brain imaging studies

- Tend to confirm basic asymmetries inferred from lesion studies, although brain activity often more bilateral than expected
- But also indicate some new twists ...

fMRI during naming of tools and animals

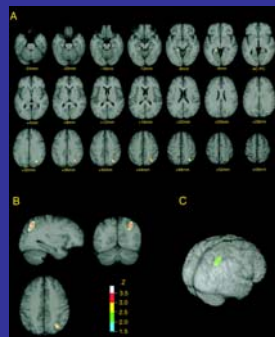


Tools left-hemispheric, animals right-hemispheric

—Chao, L. L. et al. (2002) *Cerebral Cortex*, 12, 545-551

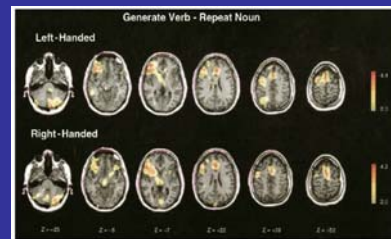
A PET study of mental rotation

- Activation in right intraparietal sulcus



Harris, I. M. et al. (2000). *Brain*, 123, 65-73

Left-cerebral dominance for sign language



- Left prefrontal activated in verb generation for both left- and right-hand signs

—Corina, D. P. et al. (2003) *J. Cog. Neurosci*, 15, 718-730

Some hypotheses about cerebral asymmetry

Crowding Hypothesis

- RH specialization occurs by default from LH deficiency, due to crowding from language
- Evidence that hemineglect results from damage to RH in region homologous to Wernicke's area, suggests Wernicke's area in LH is deficient in mediating spatial awareness

—Karnath, H.-O., et al. (2001) *Nature*, 411, 950-3.

Developmental-gradient Hypothesis

- 0 to 2-3 years: right hemisphere growth
—Chiron, C., et al. (1997) *Brain*, 120, 1057-1065
- 2-3 to 5 years: left hemisphere growth
—Thatcher, R. W., et al. (1987) *Science* 236:1110-3
- 5-13 years: right hemisphere growth?

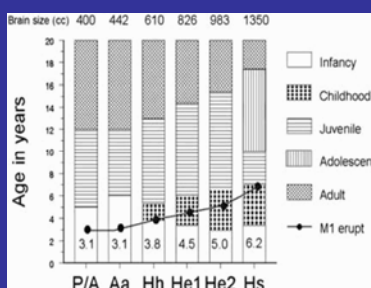
Lateralization biased in favor of growing hemisphere

Developmental-gradient Hypothesis

Can help explain

1. Equipotentiality
2. Right-hemisphere dominance for late language (e.g., Genie)
3. Sex differences in laterality?

The uniqueness of human childhood



- Language, ToM, self, episodic memory, MTT all emerge by around age 4
- Childhood may be the key to recursive thought

Locke, J., & Bogin, B. (2006). *Behav. Brain Sci.*, 29, 259-325

Frequency Hypothesis

- Left hemisphere “tuned” to high spatial frequency, right hemisphere to low spatial frequency
- Left hemisphere “tuned” to high temporal frequency (phonemes, rhythm), right hemisphere to low temporal frequency (prosody, melody)

—Ivry, R.B. & Robertson, L.C. (1998). *The two sides of perception*. MIT Press.

Spatial-Frequency Hypothesis:

LH better at detecting "R", RH better at detecting "M"



"Generativity" Hypothesis

- "Generative assembling device" (GAD) in the left hemisphere
- Responsible for generative syntax, manufacture, partwise representations of objects
- Right hemisphere operates on holistic or non-decomposable representations

—Corballis, M. C. (1991). *The lopsided ape*. New York: Oxford

Generativity and recursion

- Generativity depends on recursion
- Recursion underlies grammar, theory of mind, episodic memory, mental time travel, manufacture
- Could it be the "glue" that binds several aspects of human cognition?

—Corballis, M. C. (2007). *American Scientist*, 95, 242-250.

Motor Hypothesis

- Left hemisphere specialized for voluntary motor production, right for emotion and perception
- Apraxia
- Language production vs reception
- Tools vs animals

—Corballis, M.C. (1998). *Trends in Cognitive Science*, 2, 152-157.

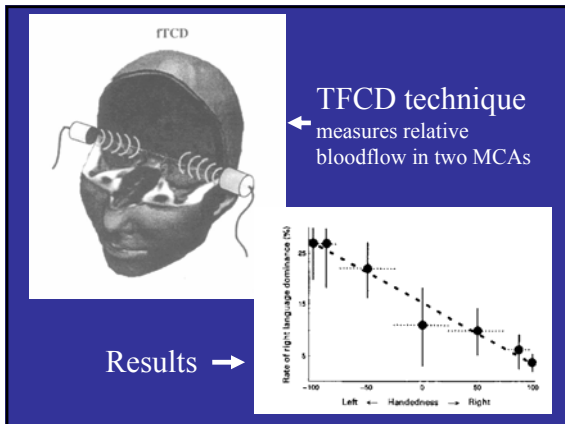
The relation of handedness to cerebral asymmetry for language

A study of handedness and language dominance

- Handedness measured by Edinburgh Handedness Inventory to give laterality quotient (LQ)
- Language dominance measured by functional transcranial Doppler ultrasonography (fTCD) during word-finding.
- Results show linear regression between % RH dominant and LQ:

$$\%RHem\ dominant = 15\% - LQ/10$$

—Knecht et al. (2000). *Brain* 123:2512-8



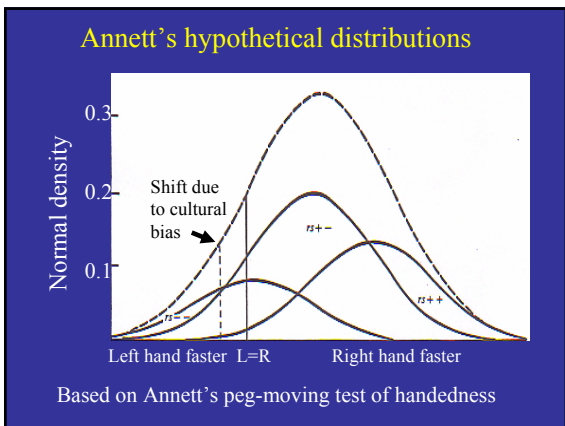
A single laterality gene?

- Annett: RS+ gene biases brain development toward right-handedness and left cerebral dominance for language
- McManus: similar theory—dextral (D) allele codes for right-handedness and left dominance for speech and language
- Chance (C) allele leaves laterality to chance

Annett's theory

- Handedness consists of superimposed normal distributions
- Two genetic alleles: RS+ shifts distribution to the right, RS- is neutral
- Three genotypes:
 RS++ → right shift $z=2$ for males, 2.4 for females
 RS+- → right shift $z=1$ for males, 1.2 for females
 RS-- → right shift $z=0$

Annett, M. (2002). *Handedness and brain asymmetry: The right shift theory*. Hove, UK: Psychology Press



McManus's theory

Dextral allele D codes for right-handedness;
 Chance allele C codes for random handedness:

Genotype	%Right-handed	%Left-brained
DD	100	100
CD	75	75
CC	50	50

—McManus, I. C. (1985). *Psychological Medicine* (Suppl. 8):1-40.

McManus version predicts parental influence

% left-handed offspring	Parental handedness		
	R-R	R-L	L-L
Observed	9.5	19.5	26.1
Predicted with $p(D) = .760$	9.45	20.24	28.87

Annett's theory would make identical prediction

Handedness and language laterality Predictions for 100 individuals based on McManus's model

	LHem	RHem
LHanded	7	3
RHanded	83	7

- Assume handedness and cerebral asymmetry independent in CD and CC genotypes
- Assume $p(D)=0.8$, $p(C)=0.2$
- This fits data showing 70% of left-handers are left-dominant for language

The “Broca-Annett Axiom”

- Proposed by Tim Crow
- A single gene accounts for right-handedness and left-cerebral dominance for language
- Unique to humans
- Accounts for language, schizophrenia, theory of mind, and human speciation
- Located in homologous regions of X and Y chromosome, in the protocadherin region

Crow, T.J. (2004). *Laterality*, 9, 233-242

Searching for the laterality gene

- DNA screening provides no evidence that the gene is on the X or Y chromosome
- This is contrary to the Broca-Annett Axiom
- Best evidence to date comes from chromosome 2, and the LRRTM1 gene

LRRTM1

(Leucine-rich repeat transmembrane neuronal 1)

- Strong link to handedness in 222 reading-disabled siblings.
- At 3 loci, 2-2-2 haplotype had 1.1 sd shift to left-handedness in relative hand-skill test
- Linkage confirmed in 105 left-handed brothers
- Derived entirely from paternal inheritance, suggesting imprinting.

Francks, C. et al. (2007). *Molecular Psychiatry* (in press)

More ...

- Paternal linkage also to schizophrenia (associated with abnormal cerebral asymmetry)
- This based on families from New York, Oxford, Canada, and an Afrikaner sample
- LRRTM1 also known to be expressed in several brain areas, including cortex.

BUT ...

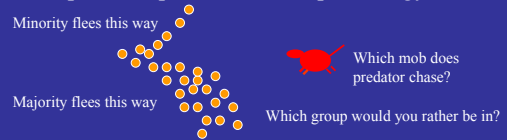
- No linkage to schizophrenia in a sample of Chinese families
- Data on inheritance of handedness suggests maternal influence is stronger than paternal influence.
- Genetic influences over handedness, schizophrenia and reading disability likely to be complex

Why polymorphism?

- Why do left-handers persist?
- Two possible answers
 - Frequency-based selection
 - Heterozygotic advantage

Frequency-based selection

- Advantage to being left-handed, but only so long as left-handers are a minority
- This can be an advantage in fights, or in competitive sports, or in escape strategy



Vallortigara, G., & Rogers, L. J. (2005). *Behav. Brain Sci.*, 28, 575-633.

Heterozygotic advantage

- CD heterozygotes have survival advantage over CC or DD homozygotes
- DD individuals strongly lateralized, with advantages in language-related activity, but disadvantages in spatial skills
- CC have the reverse pattern
- CD have the best of both

Annett, M. (2002). *Handedness and brain asymmetry: The right shift theory*. Hove, UK: Psychology Press



CC = Charlie Chaplin
Left-handed, but silent



DD = Donald Duck
All quack and no direction



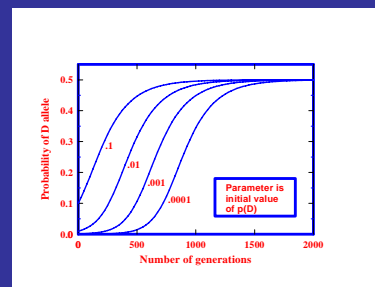
CD = Charles Darwin
Fittest of them all

Spread of a gene under heterozygotic advantage

- Suppose a mutation results in a new genetic allele D
- If CD genotype has a slight adaptive advantage, the D gene can spread rapidly through the population

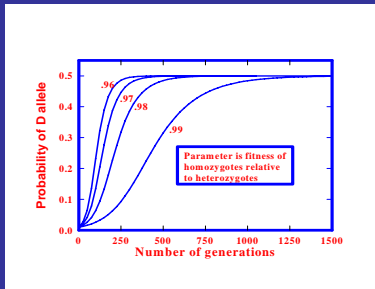
Growth in Probability of D Allele

Relative fitness of homozygotes = .99

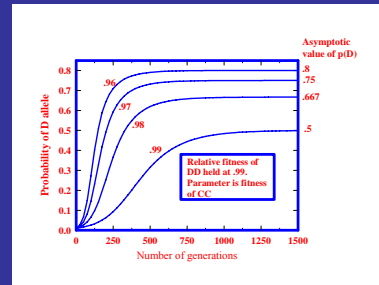


Corballis, M.C. (1997). *Psychological Review*, 104, 714-27.

Growth in Probability of D Allele Initial probability of D allele is .01

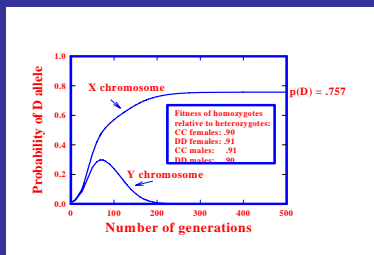


Growth in Probability of D Allele Relative fitness of DD homozygotes held at .99



Note: This can explain cultural variations

Growth in Probability of D Allele Assuming D allele in homologous locations on X and Y chromosomes



This argues against Crow's idea that gene is on X and Y chromosomes

Handedness, ability, and personality

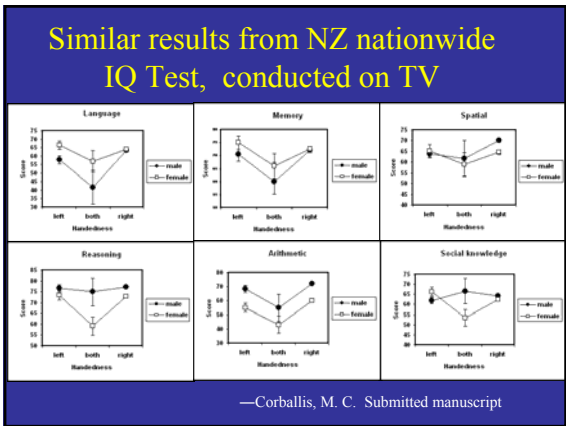
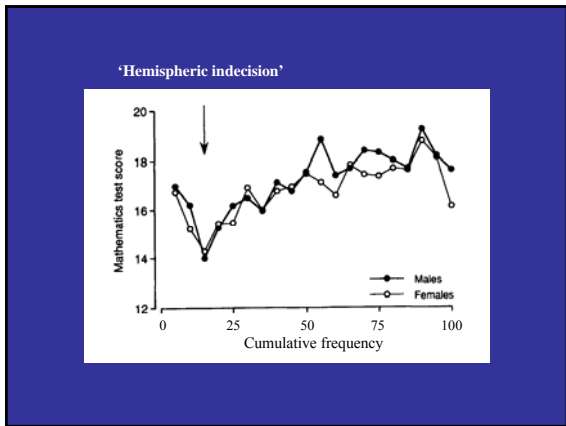
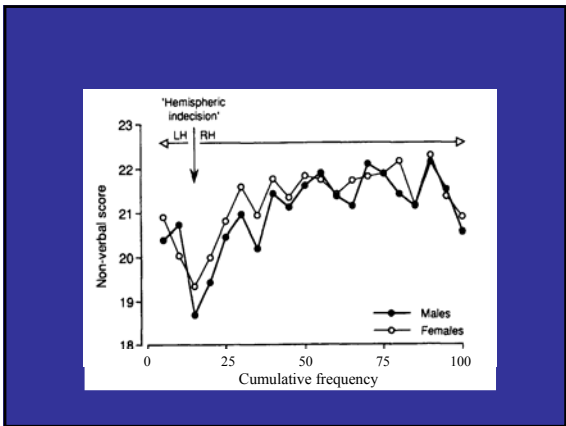
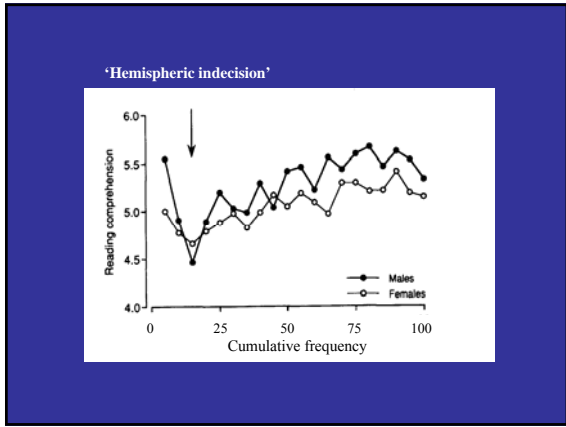
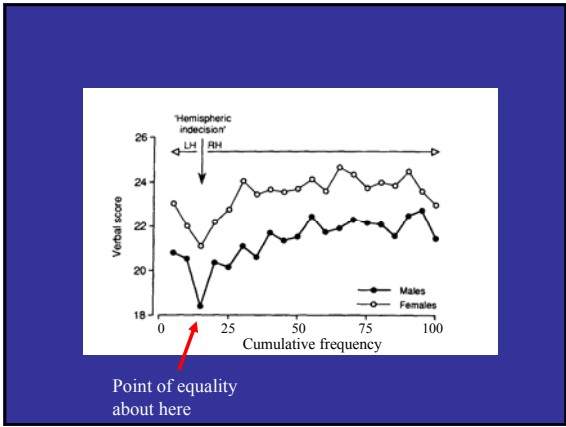
Handedness and academic ability

- 12,770 11-year-olds in UK national survey tested on:
 - Verbal ability (choose 4th word for logical, semantic, or phonological sequence)
 - Nonverbal ability (insert missing shape)
 - Math ability (arithmetic, logic, geometry)
 - Reading ability
- and also given handedness test (checking squares with each hand)

Crow, T.J. et al. (1998) *Neuropsychologia*, 36, 1275-1282

Results

- Dip on all scales at “point of equality” between the hands
- This suggests deficit in CC individuals



Conclusion?

Laterality leads to more focused thought, executive control, mental discipline ...

D allele increased probability of (left) hemispheric control.

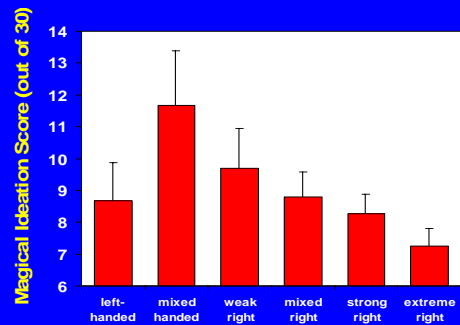
BUT why does the C allele persist?

Magical ideation and handedness

- 250 Psychology students
- Given Edinburgh Handedness Inventory
- And a test of “magical ideation” (questions of superstitions, conspiracy theories, dream interpretation, etc)

—Barnett, K. J. & Corballis, M. C. 2002. *Laterality*, 7, 75-84.

MAGICAL IDEATION AND HANDEDNESS

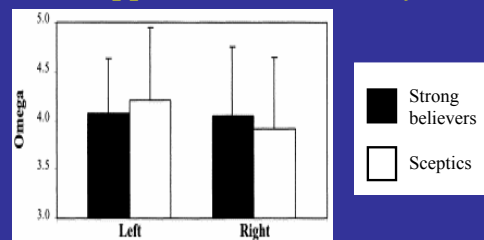


But note...

Correlation of magical ideation with *absolute* handedness, though significant ($p = .001$), explains only 4.5% of the variance. Hence a strong social or cultural component.

BUT a slight advantage in fitness can still have decisive effect on gene selection

Support from EEG study



“Omega complexity” (measure of EEG complexity) are evenly distributed between hemispheres in believers of paranormal

—Pizzagalli, D. et al. (2000) *Psychiatry Res.-Neuroimaging*, 100, 139-154

Julian Jaynes

- Left-hemisphere specialization emerged in 2nd millennium BC in response to assorted catastrophes (floods, eruptions, migrations, conquests
- Emergence of left-hemispheric “self”, responsibility for action.
- Earlier action governed by hallucinations, voices of Gods,

—Jaynes, J. (1976). *The Origins of Consciousness in the Breakdown of the Bicomeral Mind*. Boston: Houghton-Mifflin

Jaynes’s theory makes no evolutionary sense, but may capture something of consequences of cerebral asymmetry or its lack. Similar idea expressed by Michael Gazzaniga: Left hemisphere is “interpreter”—“feeling of responsibility for action”

—Gazzaniga, M. S. (2000) *Brain*, 123, 1293-1326

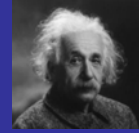
Lack of cerebral dominance associated with ...

- CC genotype?
- Magical ideation
- Schizotypy ... and schizophrenia
- Hallucinations?

BUT ALSO PERHAPS

- Lateral thinking
- Creativity

Albert Einstein



- Probably right-handed BUT
- Slow to develop speech
- A slow learner
- Central and parietal regions of his brain show “..unusual symmetry between the hemispheres ..” (Witelson *et al.* 1999, p. 2151)

Witelson, S. F., et al. (1999). *The Lancet*, 354, 2149-2153

Leonardo da Vinci

- Inventive genius
- Artist, scientist, engineer
- Left handed
- Wrote in mirrored script



“I have long had a suspicion that mankind is indebted for much of its individuality and for certain forms of genius to individuals [with] some predisposition to insanity. They have often taken up the by-paths of thought, which have been overlooked by more stable intellects.”

—Henry Maudsley (1871) *Body and mind*. NY: Appleton

Creativity and Insanity

Bartok, Beethoven, Ravel, Warlock ...
Flaubert, Nietzsche, Ruskin, Strindberg ...
Lawrence, O’Neill, Proust, Thomas ...
Modigliani, Utrillo, Van Gogh ...

Conclusion

- Classic dichotomy between linear and lateral thinking
- NOT a question of left- vs right-hemisphere
- RATHER, a question of symmetry vs. asymmetry
- D → lateralization; C → symmetry
- CD heterozygotes have combination of both

Is laterality uniquely human?

Handedness and cerebral asymmetry still widely assumed to be uniquely human

- Annett (*Handedness and brain asymmetry: The right shift theory*. Hove, UK: Psychology Press, 2002)
- Corballis (*The lopsided ape*. NY: Oxford, 1991)
- Crow (*Laterality*, 9, 233-242.)
- McManus (*Right hand, left hand*. London: Phoenix, 2002)

BUT ...

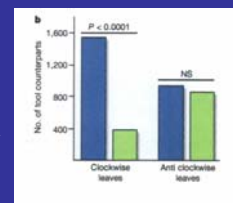
Tool manufacture in crows



Crows strip tools from Pandanus leaves like this →

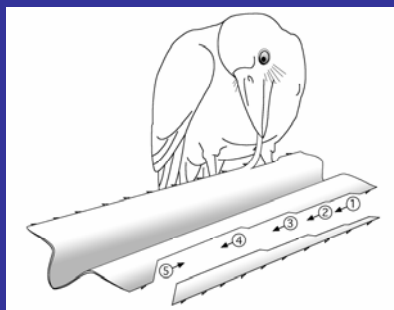


← ...and this shows the bias toward the right eye, or left hemisphere



—Hunt et al. (2002)

Birds mostly view with the RIGHT EYE when making tools, implying dominance of the LEFT BRAIN



Evidence for left-hemispheric control of vocalization in:

- Frogs (Bauer, R. H. (1993). *Psychobiology*, 212, 243-248)
 - Marmosets (Hook-Costigan, M. A. & Rogers, L. J. (1998). *Neuropsychologia*, 36, 1265-1273)
 - Songbirds (Nottebohm, F. (1972). *J. Exp. Zoology*, 179, 25-50)
- AND
- Enlarged Broca's area on left in 14/20 chimpanzees (Cantalupo, C. & Hopkins, W.D. (2001). *Nature*, 414, 505)

Evidence for left-hemispheric dominance for perception of species-specific vocalization in:

- Mice (Ehert, G. (1987). *Nature*, 325, 249-51)
- Rhesus monkeys (Hauser, M. D. & Anderson, K. (1994). *Proc. Nat. Acad. Sci., USA*, 91, 3946-3948)
- Japanese macaques (Heffner, H. E. & Heffner, R. S. (1984). *Science*, 226, 75-76)
- Chimpanzees (Gannon, P. J., et al. (1998). *Science*, 279, 220-221)

Evidence for right-handedness in:

- Toads (Bisazza, A., et al. (1996). *Nature*, 379, 408)
- Walruses (Levermann, N., et al. (2003). *BMC Ecology*, 3, 9)
- Chimpanzees (Hopkins, W. D., et al. (2004). *Behav. Neurosci.*, 118, 659-663)

Broca-Annett Axiom?

- Single gene for handedness and cerebral asymmetry? **Increasingly unlikely**
- Unique to humans? **Probably not**
- Accounts for language, schizophrenia, theory of mind, and human speciation? **As a single mutation, probably not**
- Located in homologous regions of X and Y chromosomes? **Very unlikely**

Nevertheless

- Bipedalism may have enhanced handedness in humans
- Increasing brain size may have enhanced cerebral asymmetry, and extended it into true language
- Cerebral asymmetry may hold the key to human variation