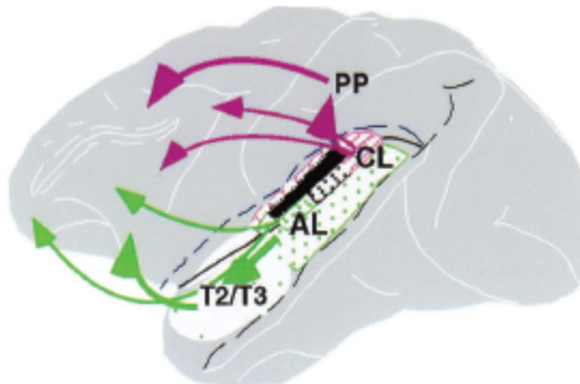
FAV, Talk no. 5, Auditory Cortex, Spatial Hearing, Speech Perception



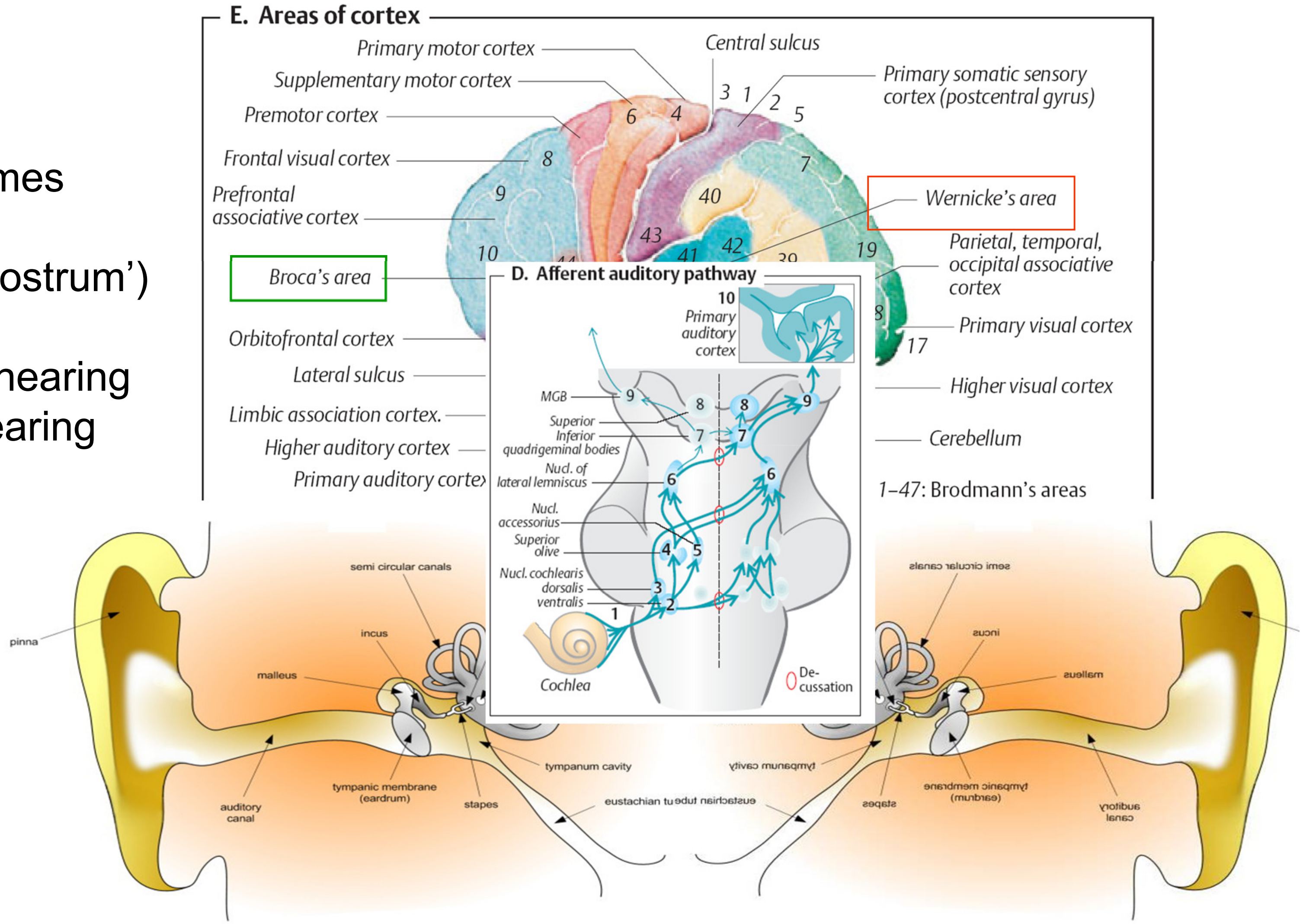
Petr Maršálek

http://onyx.lf1.cuni.cz/mlab/ftp/PPT-CVUT/FAV/2022

September/ October 2022

Overall view at the auditory pathway

Auditory pathway
from the two ears
crosses several times
at different height
(= distance from 'rostrum')
Crossings:
1) back up object hearing
2) serve spatial hearing



Auditory pathway
from cochlea to
brainstem
and subcortical
centers
to thalamus and
cortex

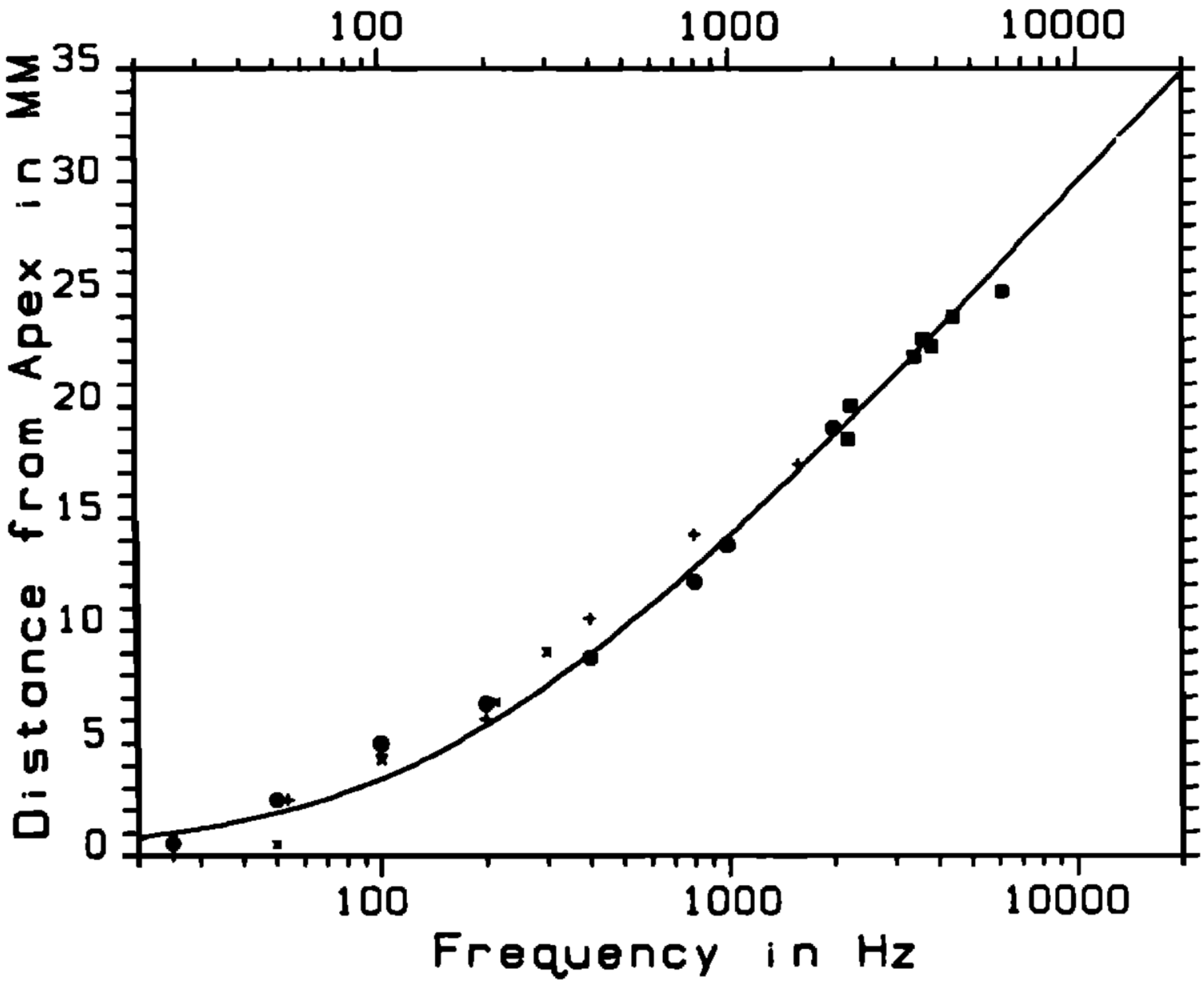
Outline FAV 5

- **Binaural hearing**
- Medial Superior Olive computes sound azimuth in horizontal plane in low frequencies from interaural time difference
- Lateral Superior Olive computes sound azimuth in horizontal plane in high frequencies from interaural intensity difference
- Cortex
- Thalamus is a gateway through which sensory stimulation gains cortical attention and processing. We can be woken up by strong auditory or visual stimuli.
- Neocortical brain areas have common features (six layers) and distinctions (sensory versus motor, and others).
- Sensory areas are typically divided into ‘primary’ and ‘secondary’, but the functional features of processing order between these remain unclear.
- There are 47 distinct Brodmann areas (by Korbinian Brodmann, 1909).
- Speech
- Distinct areas enable vocalization: 2 major speech centers, sensory and motor.
- Inter-hemispheric division of labor: when we sing a song, left (dominant) hemisphere maintains lyrics and the other (non-dominant) hemisphere contains the melody.
- Speech sounds (vowels, consonants) have distinct spectral and temporal features (formants).
- There are critical developmental periods for speech acquisition – language understanding starts before speech production. Developmental period partly closes in puberty.
- (Families of Indo-European languages, tonal languages, language origin, structure and putative universal grammar et cetera. This is fascinating, but it is mostly beyond scope of these lectures…)
- Hearing loss in ageing progresses across modalities and higher loudness in hearing aid often does not help – is there a need for augmented media? Yes…

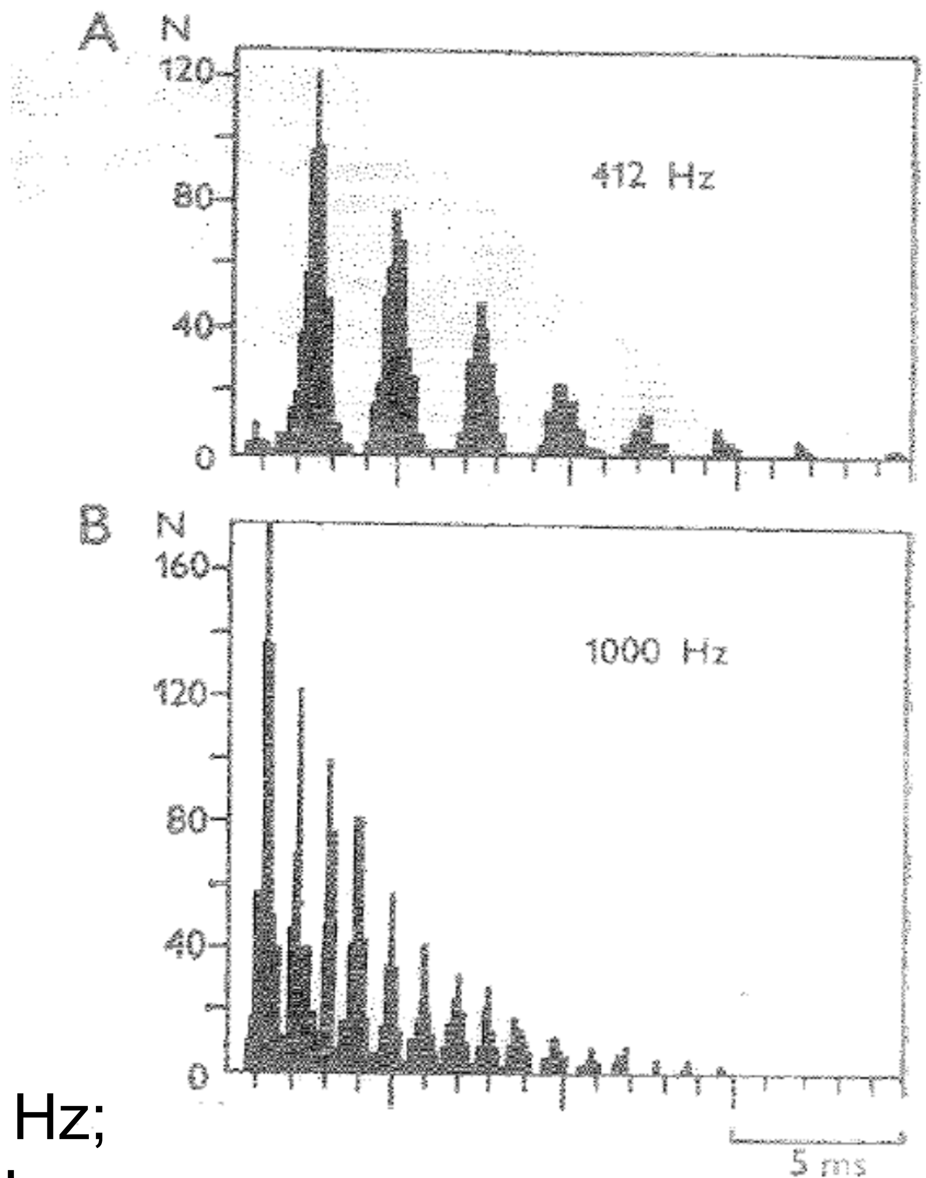
Outline - Binaural hearing

1. Introduction: coincidence detectors are part of the circuit
2. Hypothetically it is possible that coincidence detectors are at different processing stages
3. Several models are discussed: with and without synaptic mechanisms, with and without cochlear mechanics, and other variants
4. Outputs of all models are evaluated by the ideal observer
5. Questions addressed/ open questions
6. Example: Can modeling phase information improve our description/ understanding of ‘medial superior olive’/ ‘interaural time difference’ mechanisms?
7. Discussion

Tonotopic organization in cochlea, function of D.D. Greenwood, 1961



auditory nerve
phase coding
interval histogram



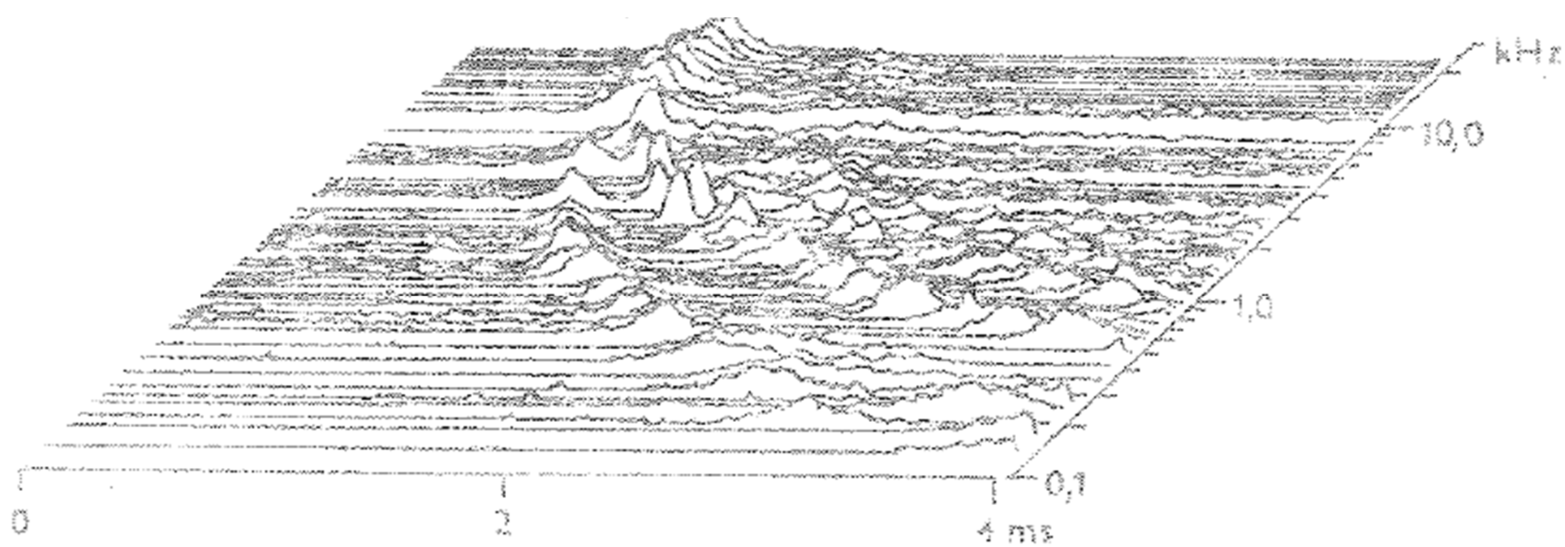
spikes are in rectified half-wave probabilities/ synchronizations

x-axis: time, ms;
y-axis: N - Number of spikes

(A) stimulation frequency 412 Hz;
(B) stimulation frequency 1 kHz.

[Rose JE, 1962]

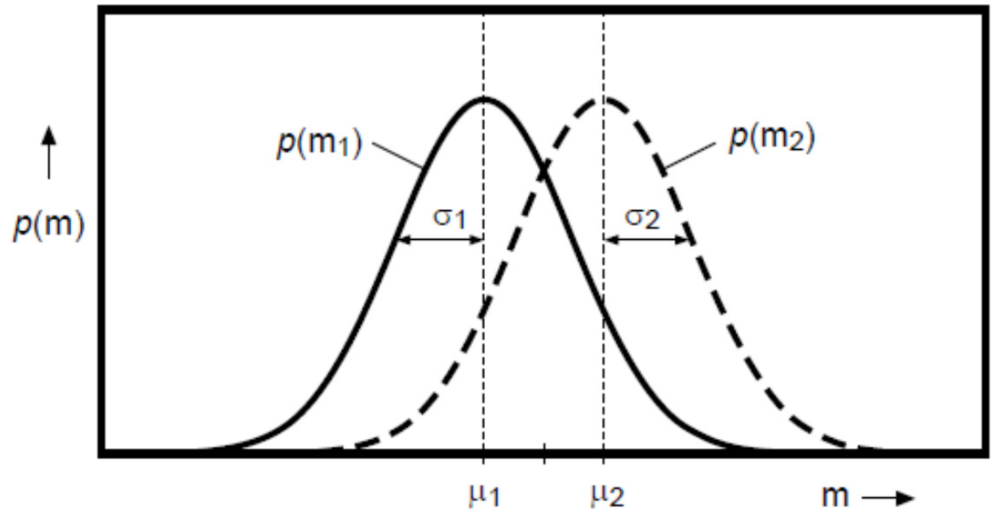
auditory nerve
time and frequency coding
time histogram



x-axis: time; y-axis: neuronal characteristic frequency;
z-axis: spike time histogram

[Kiang, 1965]

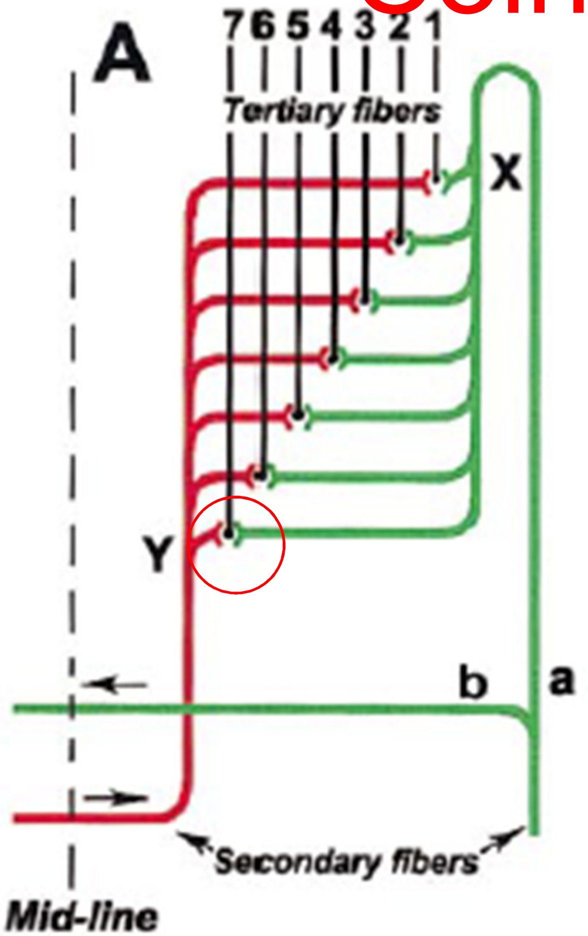
Signal discrimination by ideal observer

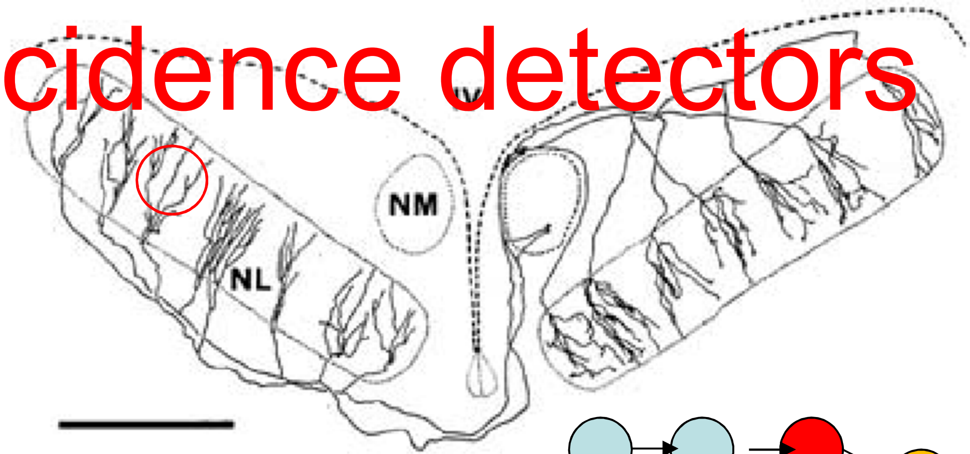


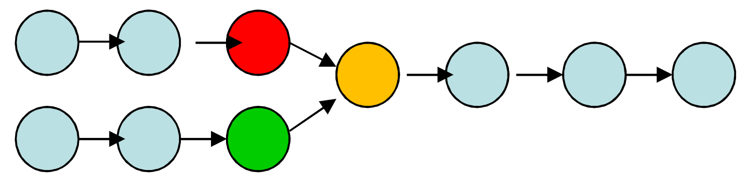
x-axis: firing rates;
y-axis: response probabilities;
- different signals are detected based on variable responses and different mean values
- JND (just noticeable difference), in dB
- encoded by spikes

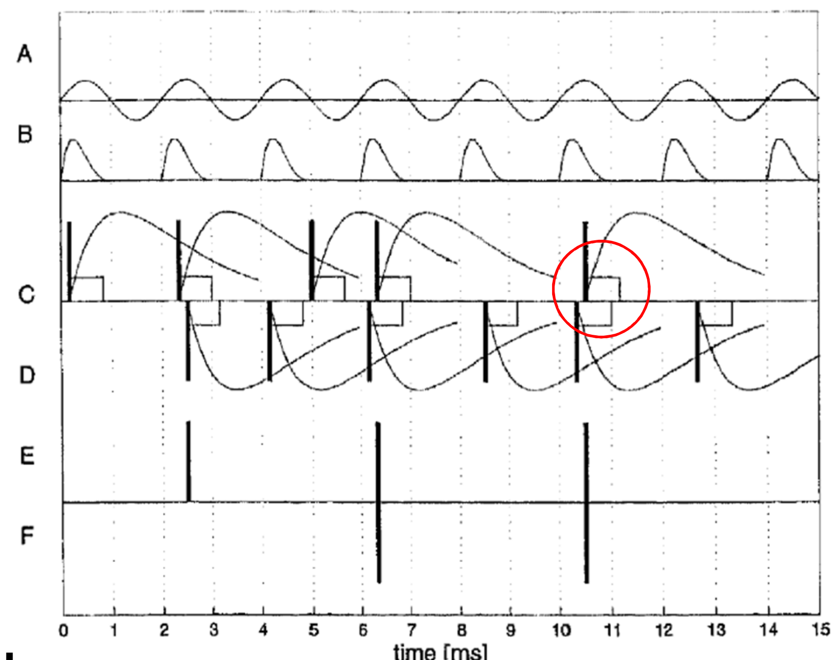
[(computational) neuroscience reviews/ textbooks]

Coincidence detectors



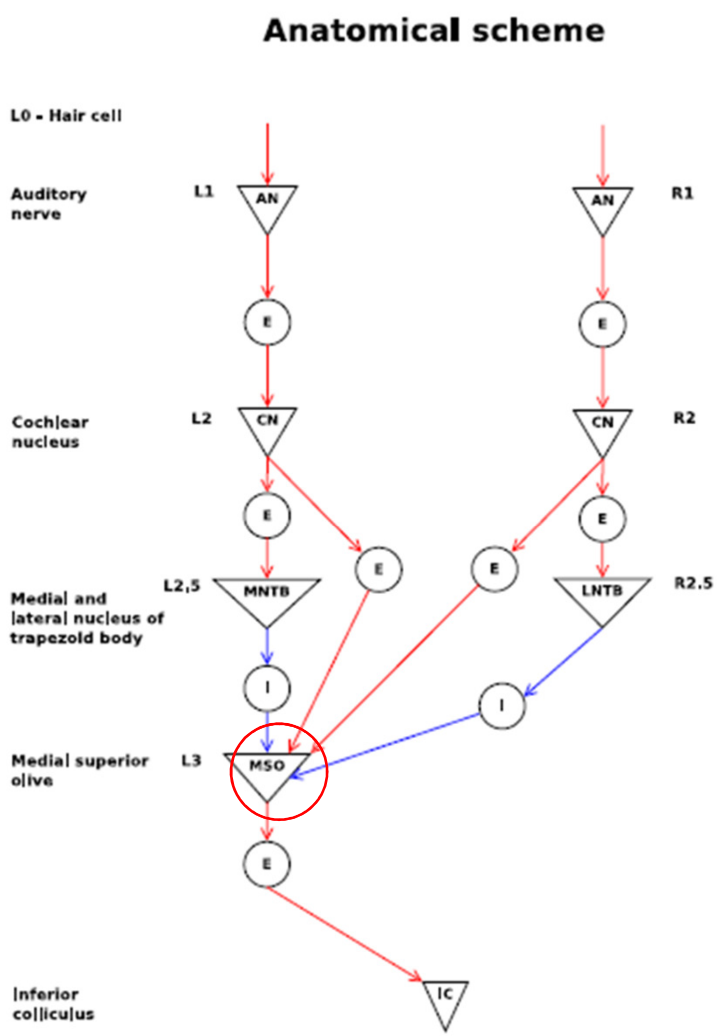


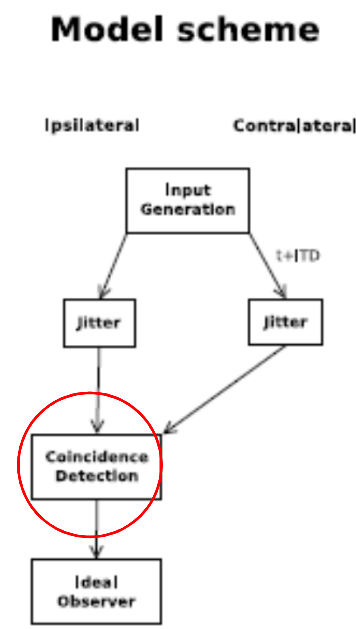




Jeffress delay line is the use of coincidence detectors in birds. Mammals use other circuitry with coincidence detectors

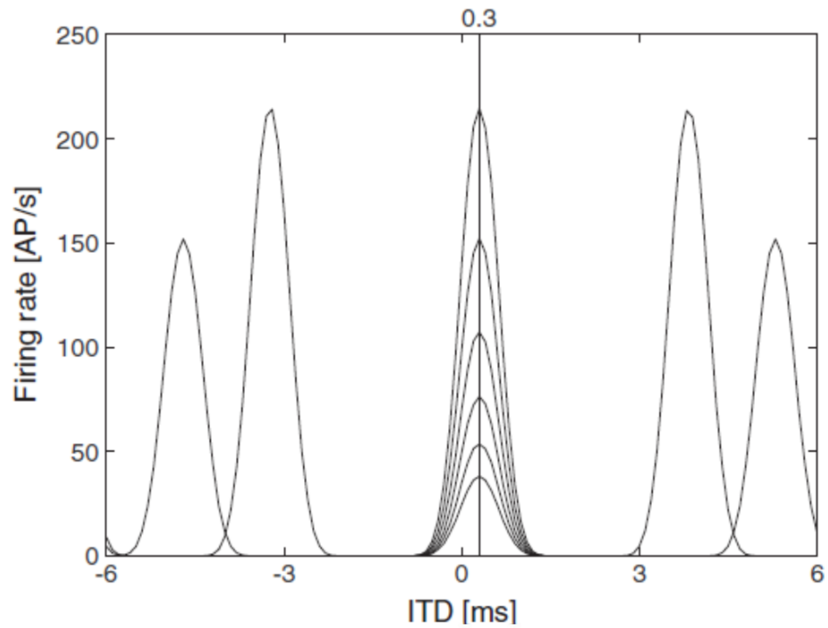
Sanda and Marsalek, Stochastic interpolation model…of MSO…, *Brain Research*, 2012.
(= model without cochlear mechanics)

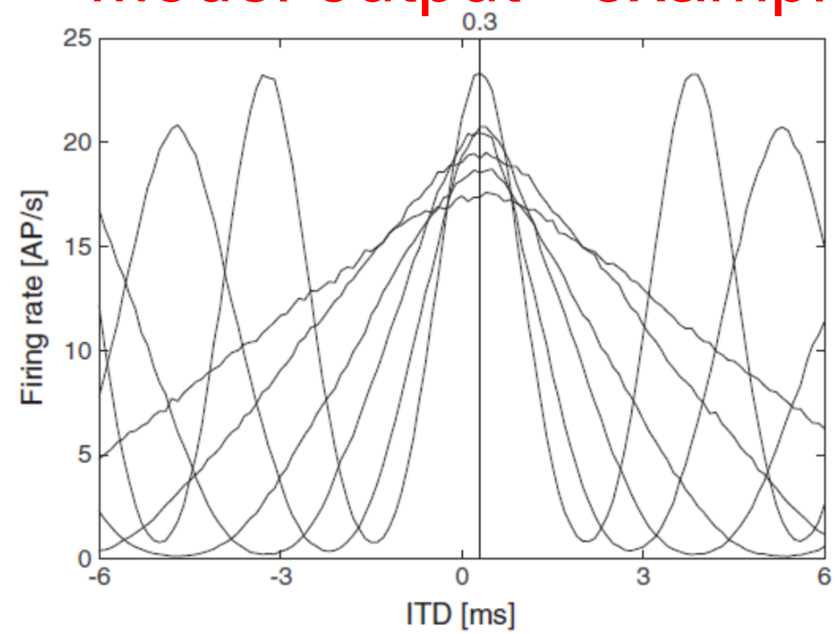


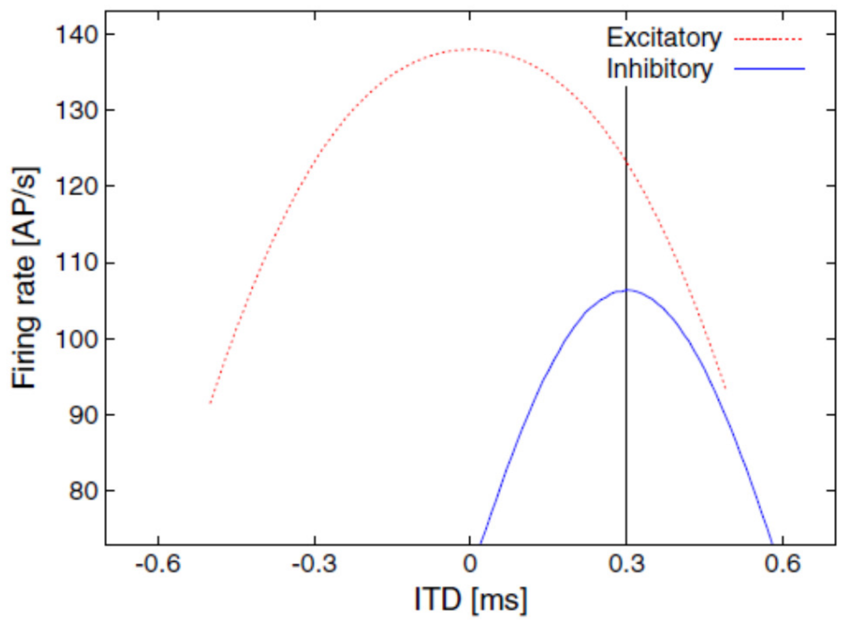


Model output - examples

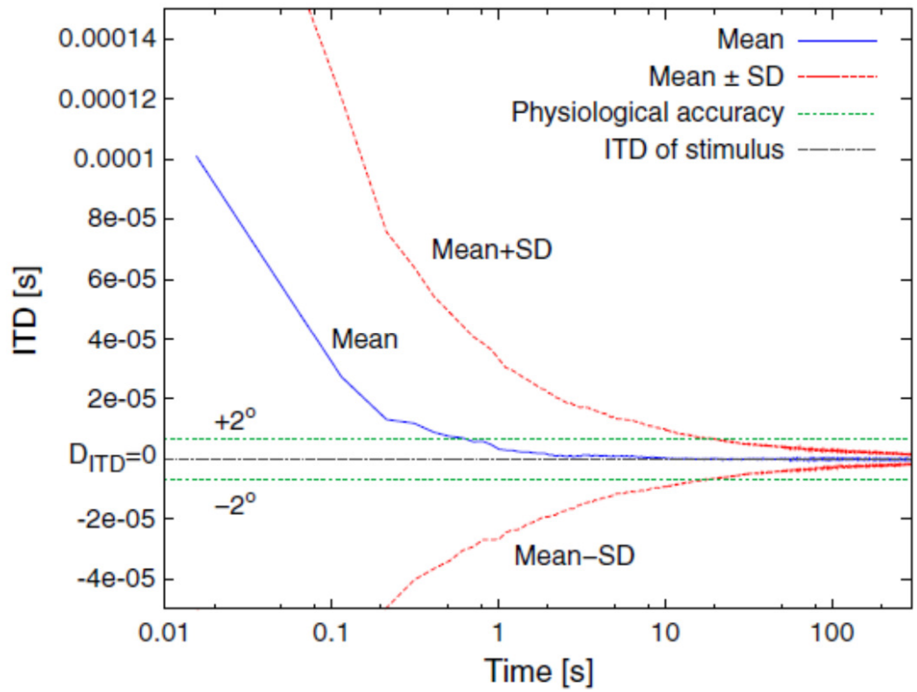
Sound frequencies 50, 71, 100, 141, 200, 283 Hz.

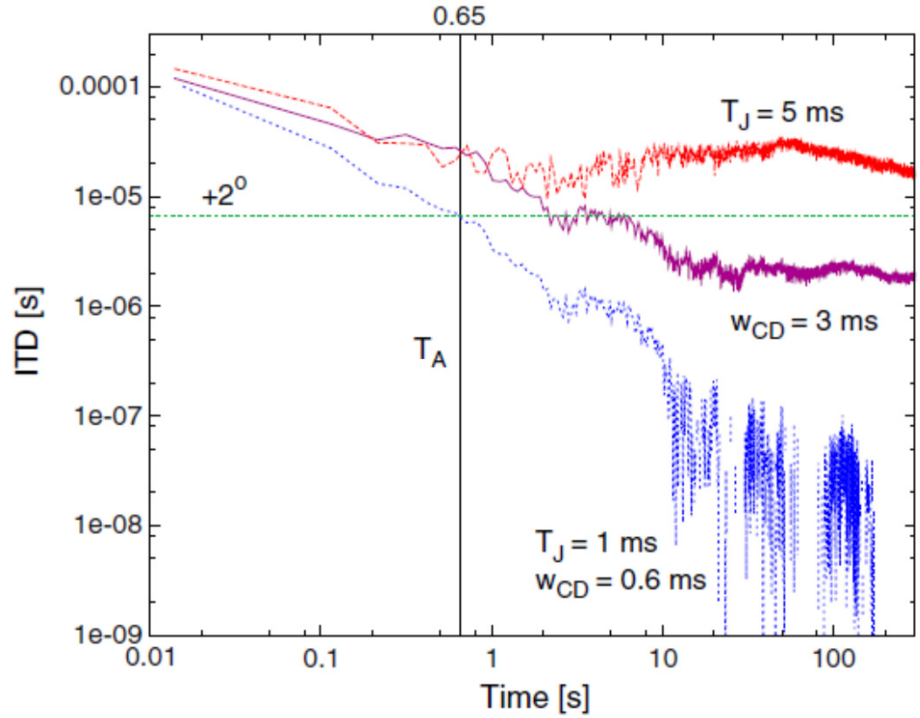


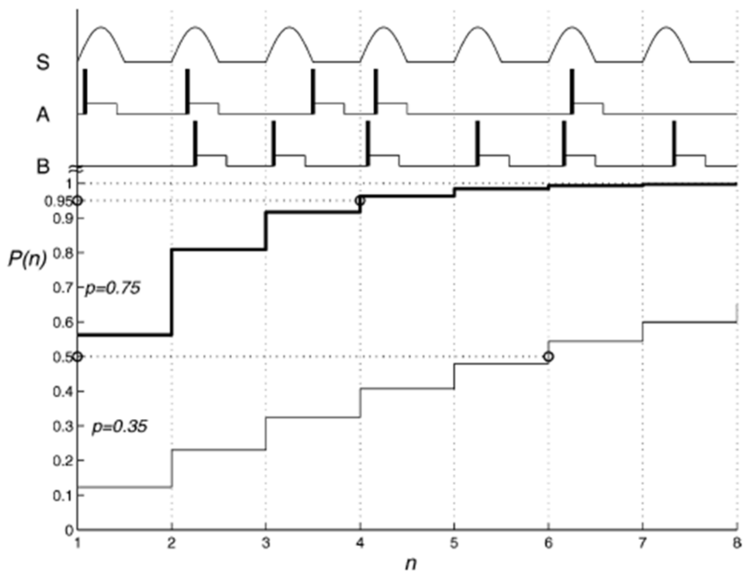




[Sanda and Marsalek, 2012]



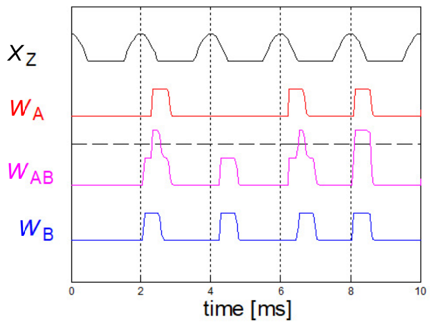


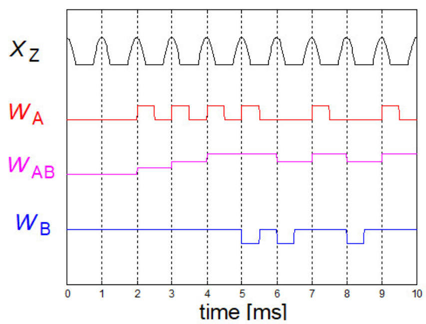


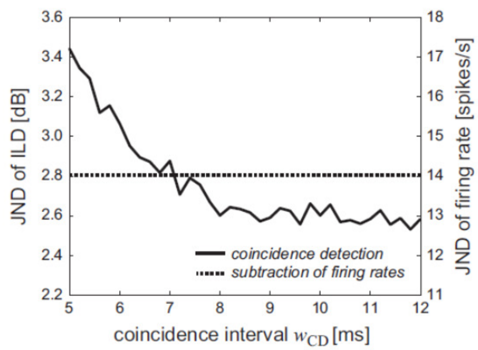
low frequency localization with several different parameter settings/ ideal observer readouts:
left: single neuron, unlimited time
right: reaction time of azimuth TA, spike timing jitter TJ, window of coincidence detection wCD

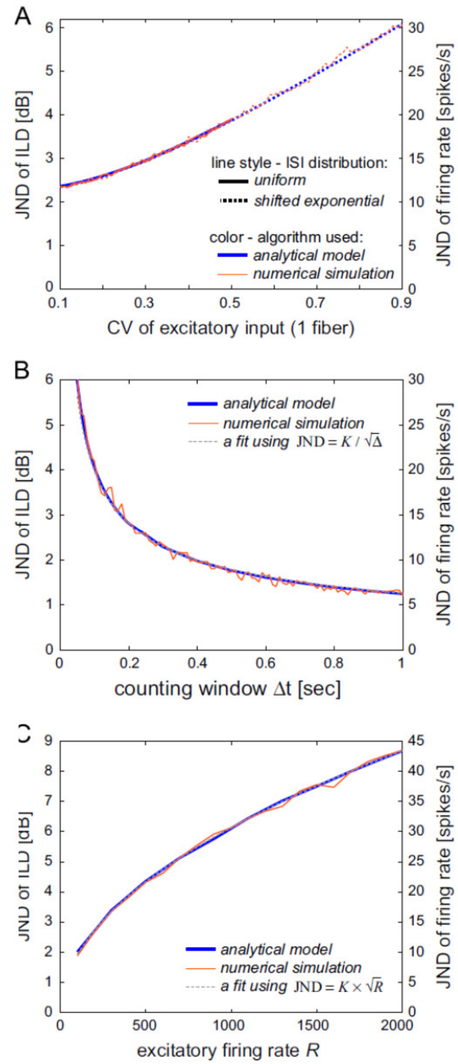
[bw: Lansky and Marsalek, 2008] [colored: Sanda and Marsalek, 2012]

Coincidence detection - examples

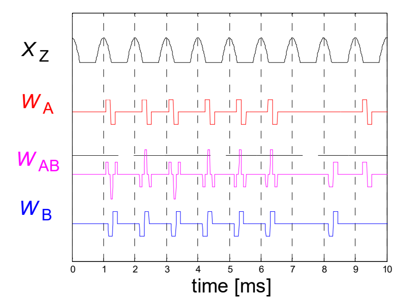




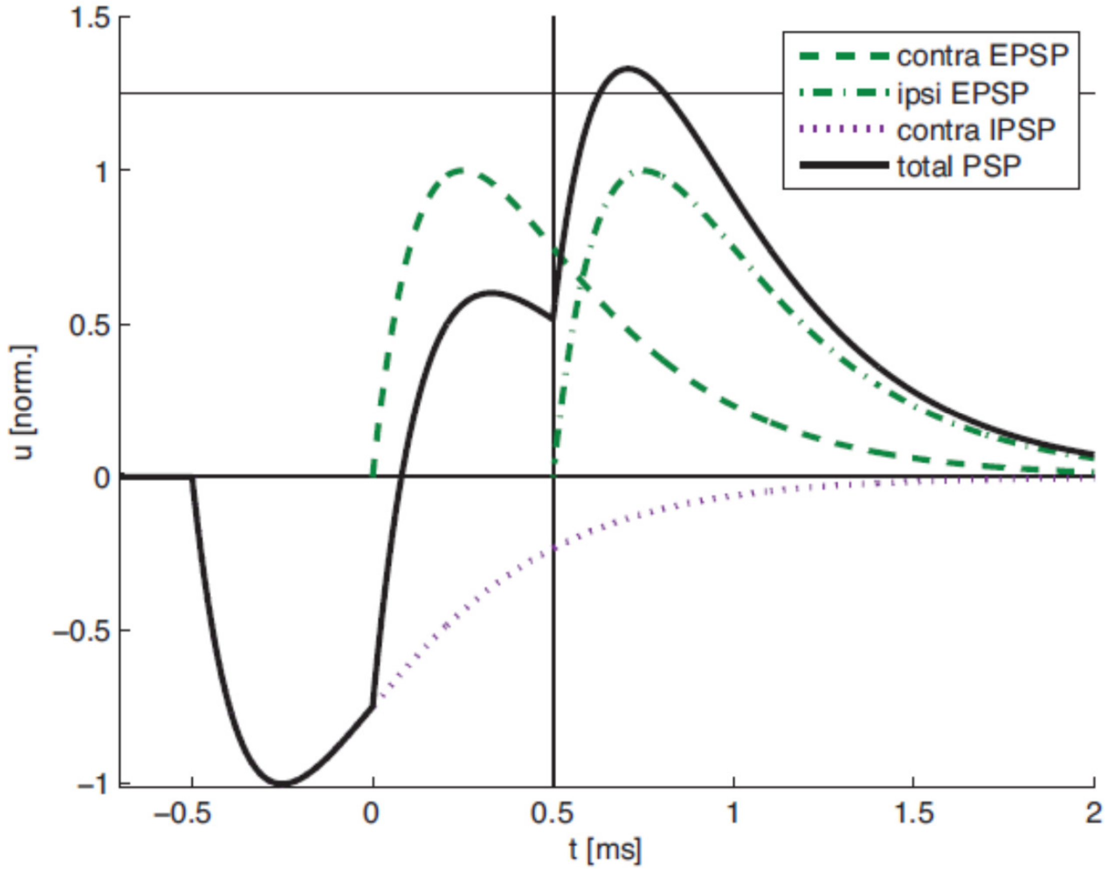




left from top: candidate mechanisms of sound azimuth in LSO, in high frequencies.
JND, just noticeable difference in ILD, inter-aural level difference can be equivalently expressed in dB, or in spikes/ s.
right: shows parameter variation.
bottom: inhibition/ post-inhibitory rebound



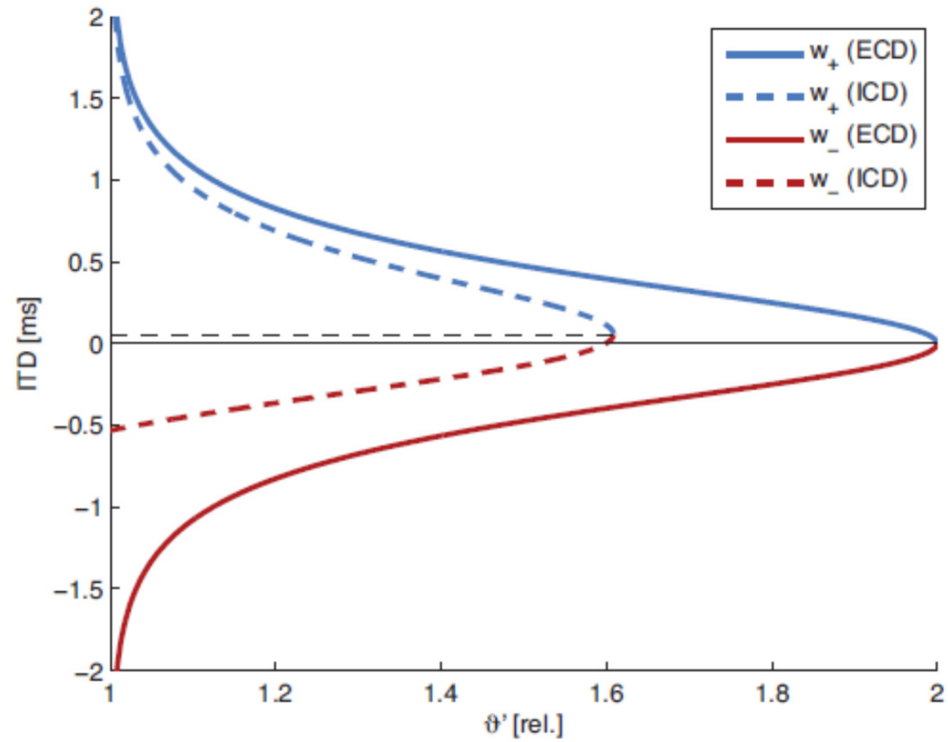
[Bures and Marsalek, 'On Lateral Superior Olive, LSO', 2013]

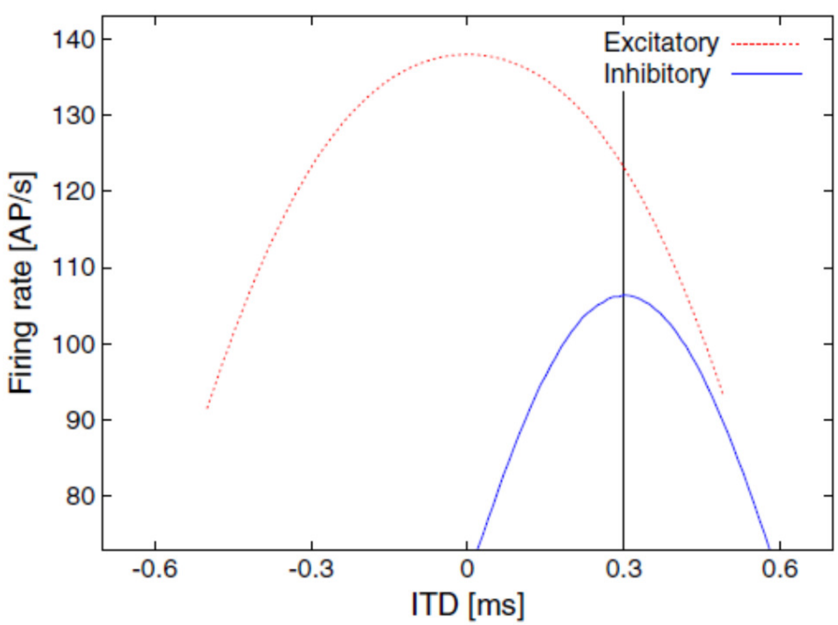


Coincidence detectors are 'implemented' by combination of few EPSPs and an IPSP.

These are candidate mechanisms of calculating sound azimuth in low frequencies with the use of adding excitatory and inhibitory postsynaptic potentials.

[Toth and Marsalek, 2015]

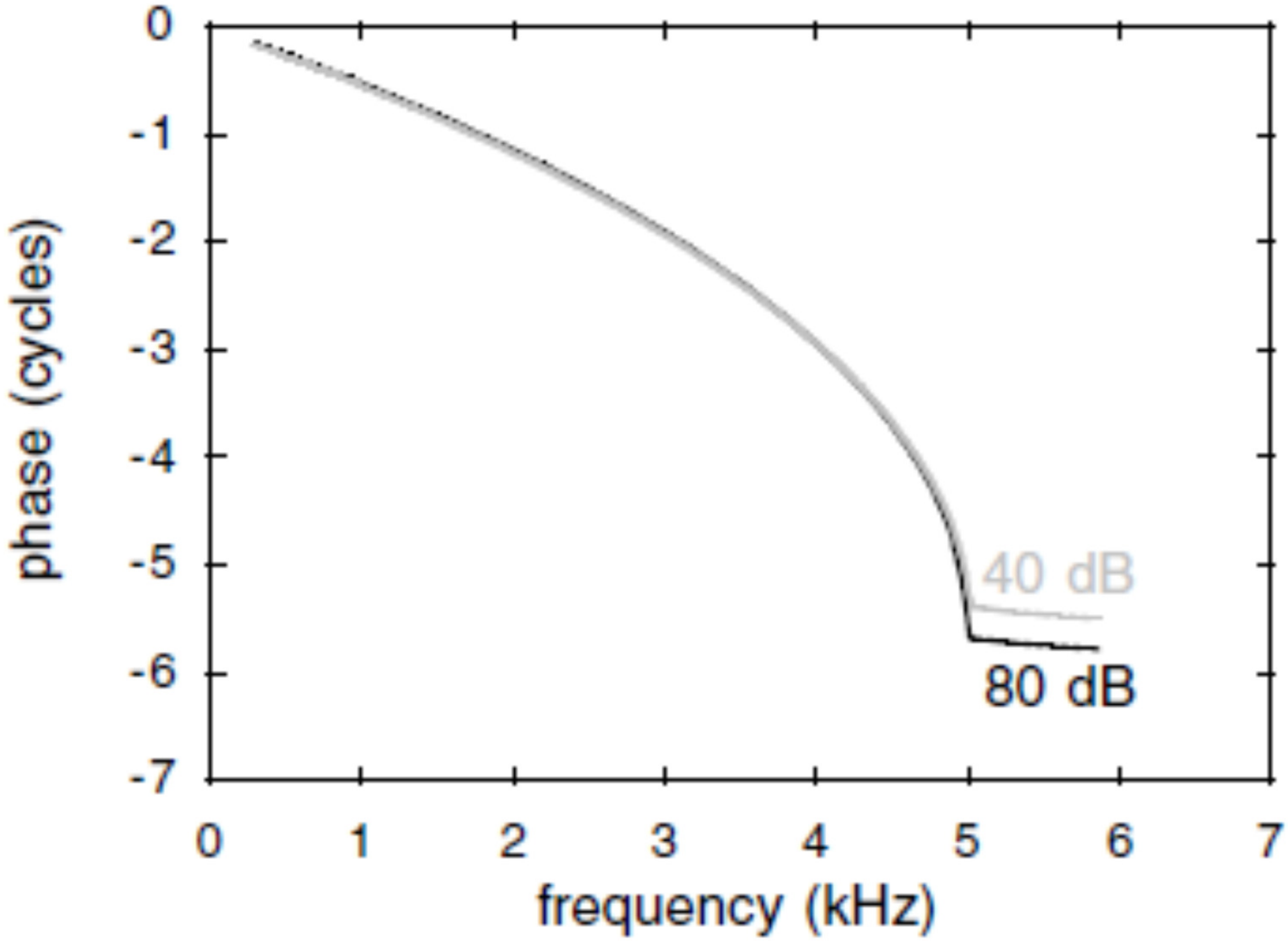




[Toth and Marsalek, 2015]

Solution to some questions as to the construction of the ‘tuning curve’ can be simple: to calculate a “read-out” curve, it just needs to take inversion function of a spike time histogram, pick a proper branch and a proper function normalization.

Cochlear phase in response to sine input



Simplified cochlear model by Duke, Julicher, Vilfan, and others

Applications of auditory nerve spike train studies: cochlear implants (CI) .
Some cochlear implantees have implants on both sides (mostly in German speaking countries). How is it with binaural hearing and horizontal localization?
In tonal languages (Asian, like Chinese) pitch by CI is the processing bottleneck. How can be pitch impression improved in CI? Key observation: tradeoff localization vs. pitch.
Ambisonics/ holophonics/ augmented/ etc/ digital sound engineering …

open problems, interdisciplinary questions, technology questions

Literature – Binaural Hearing

BURES Z. and MARSALEK P., Models and manuscripts in preparation.

TOTH P.G. and MARSALEK P., Analytical description of coincidence detection synaptic mechanisms in the auditory pathway. *Biosystems*, 136, 90-98, 2015.

BURES Z. and MARSALEK P., On the precision of neural computation with inter-aural level differences in the lateral superior olive. *Brain Res.*, 1536, 16-26, 2013.

SANDA P. and MARSALEK, P., Stochastic interpolation model of the medial superior olive neural circuit, *Brain Res*., 1434, 257-265, 2012.

MARSALEK P., DRAPAL M., Mechanisms of Coincidence Detection… Chapter in Book: *Mathematical Modeling of Biological Systems*, 2008.

BURES Z., PhD thesis, 2007.
MARSALEK P., Habilitation thesis, 2005.

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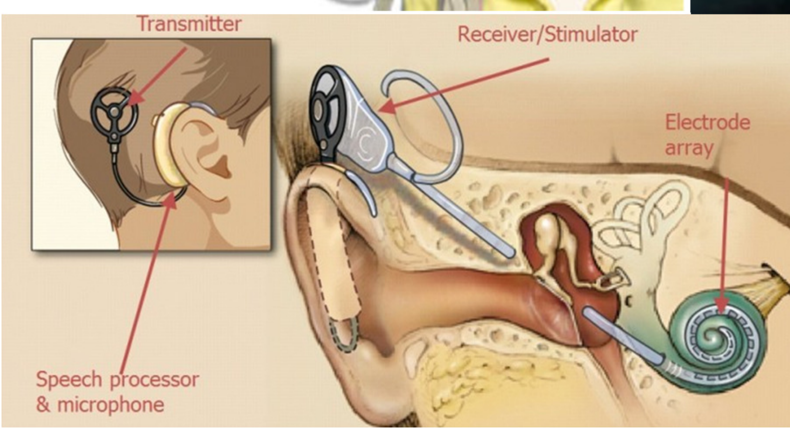
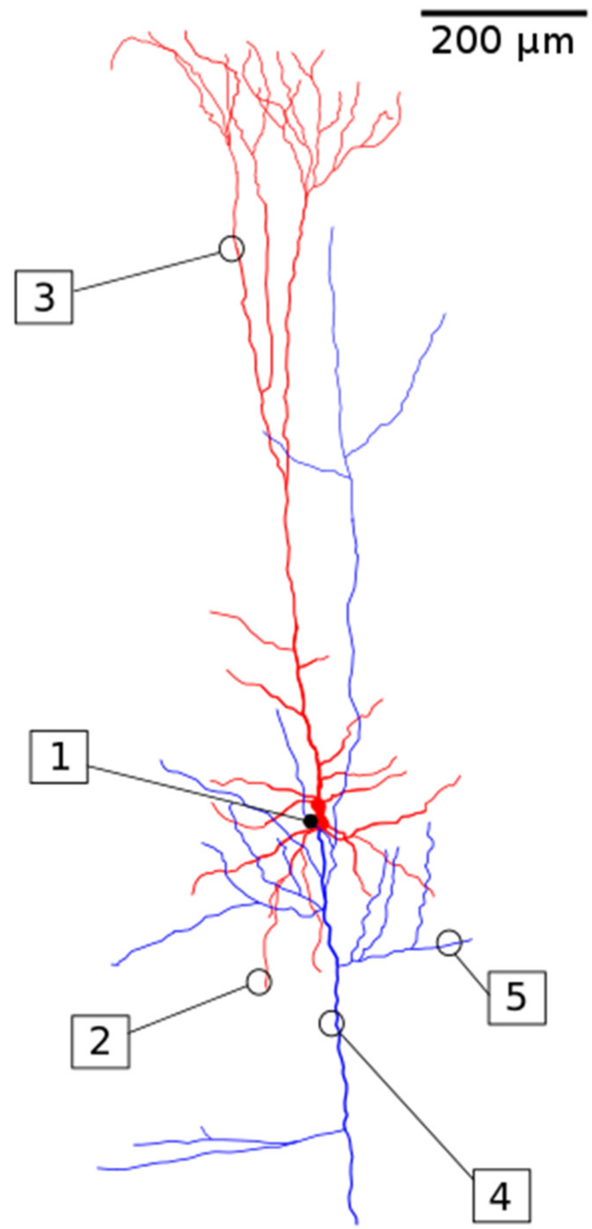
How Do We Collect Information About Cortex? We Use Electrophysiology, Non-invasive and Invasive.

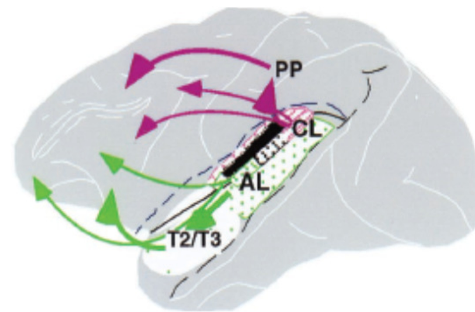


Pyramidal Neuron

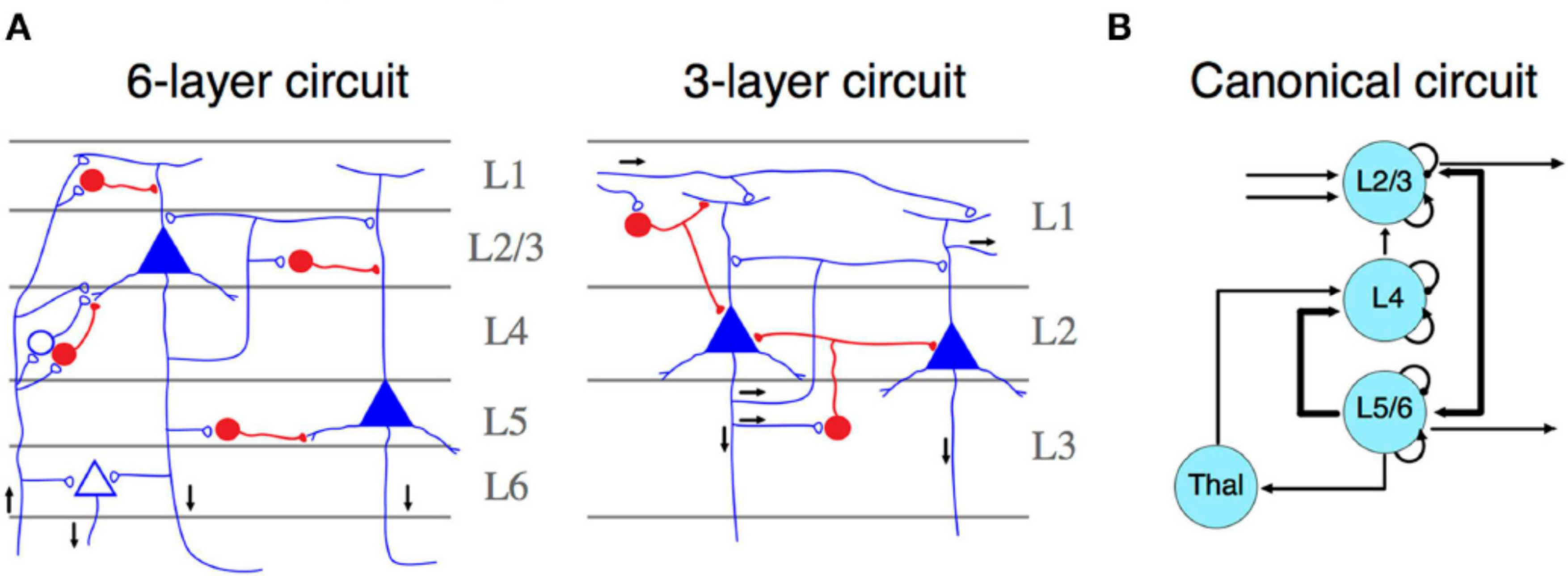
As most neurons, this cell consists of:
[1] cell body
[2] basal dendrites
[3] apical dendrites
[4] principal axon
[5] axon collaterals
Synapses use excitatory neuro-transmitter: glutamate.



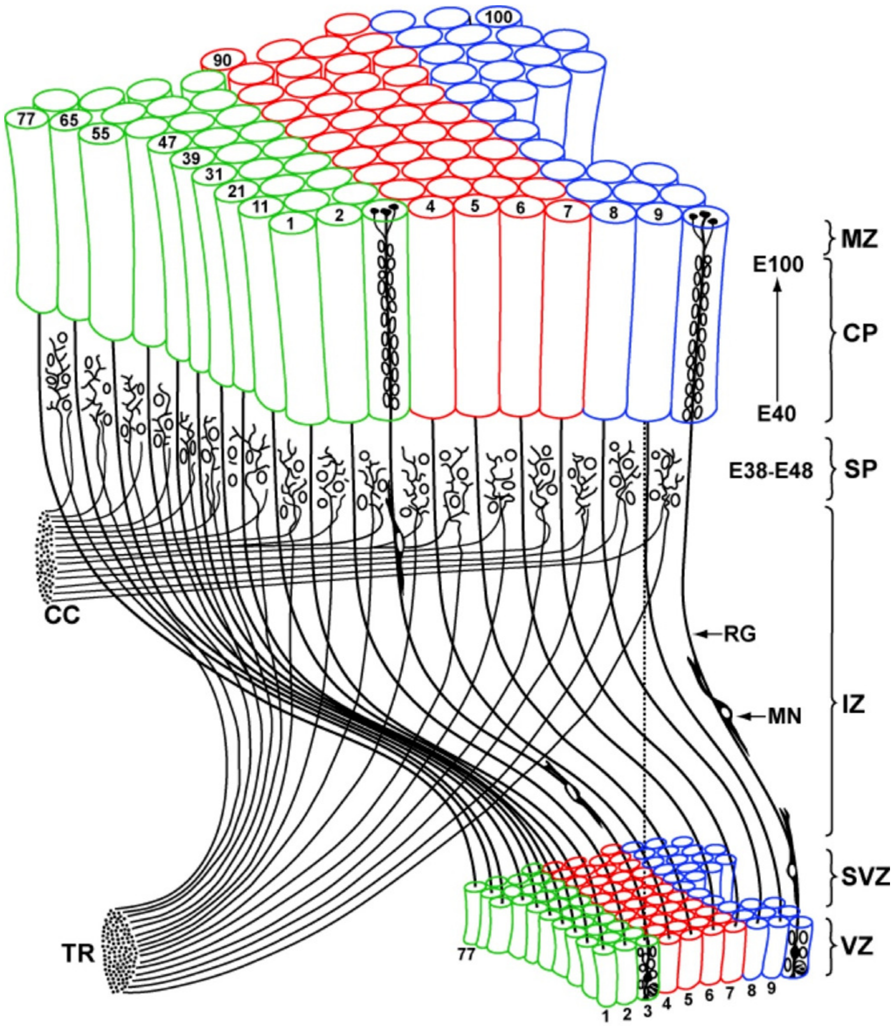
CORTICAL MICROCIRCUIT



Neocortex and Other Cortices (Paleocortex, Olfact. Only: 3 Layers, Archicortex, Olfact. and Hippocampus, 3 or 4 Layers)



Cortex Consists of Columns as Functional Units



Area of Cerebral Cortex Correlates with the Size and Surface Area of the Mammal

CC = Cortico-Cortical Connections, TR = Thalamic Radiation

Skid Time

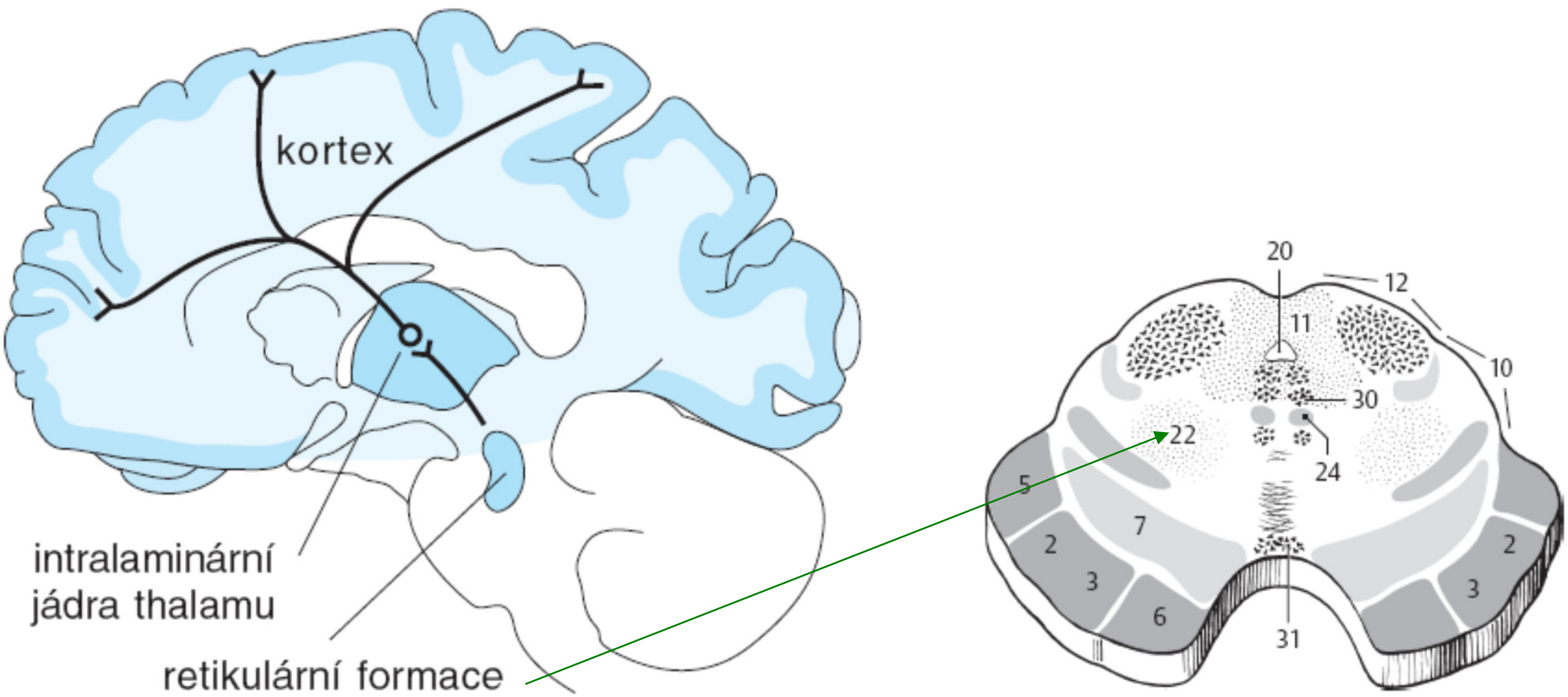
Unfolded Human Cerebral Cortex Has Surface Area As Medium Size Pizza

Says Our Proud Pastafarian Mission

Cerebral Cortex and Other Connected Nuclei

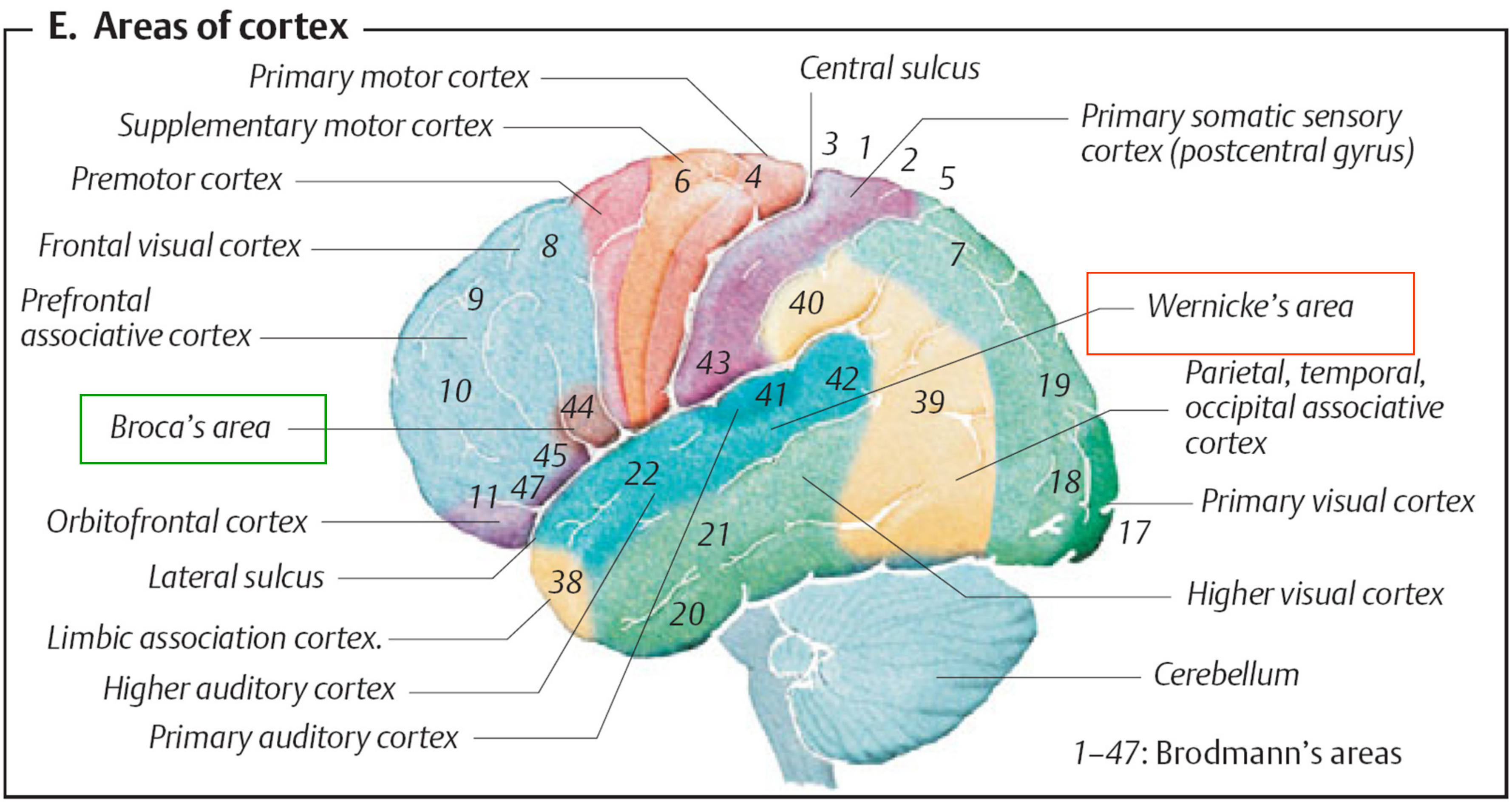
- Reticular Formation
- Sensory Projections
- Motor Projections
- Thalamus
- … Other Sub-Cortical Projections...

Reticular Formation



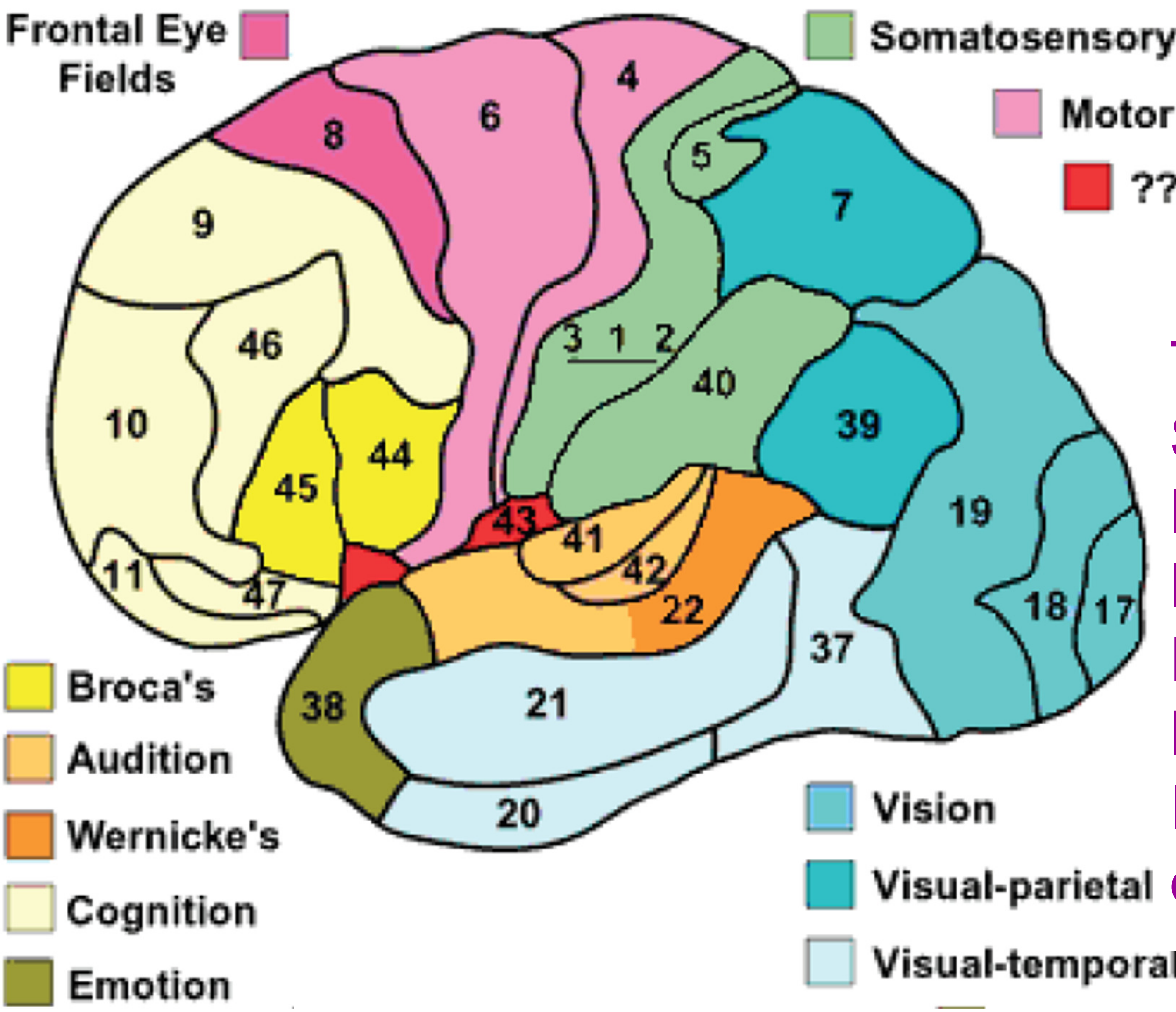
C Section through inferior colliculus

Two Main Speech Centers Within the (Brodmann's) Areas



Despopoulos, Color Atlas of Physiology © 2003 Thieme

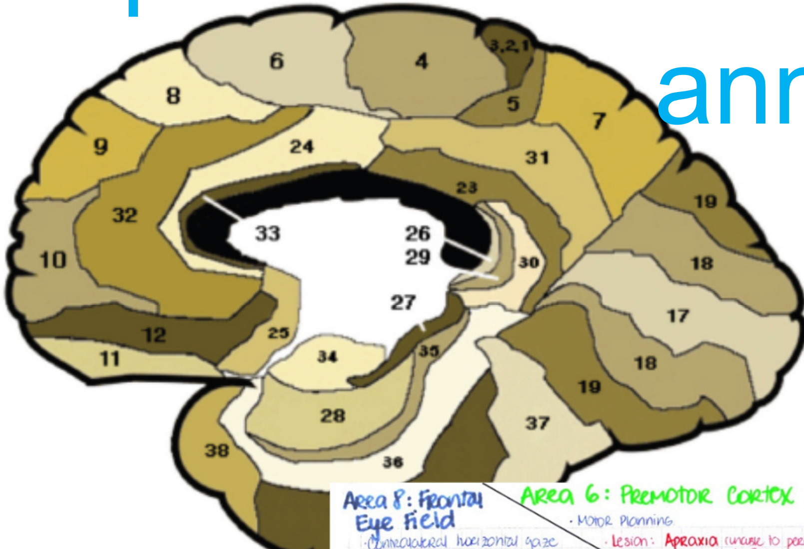
Brodmann Areas (Outer Hemisphere Part)

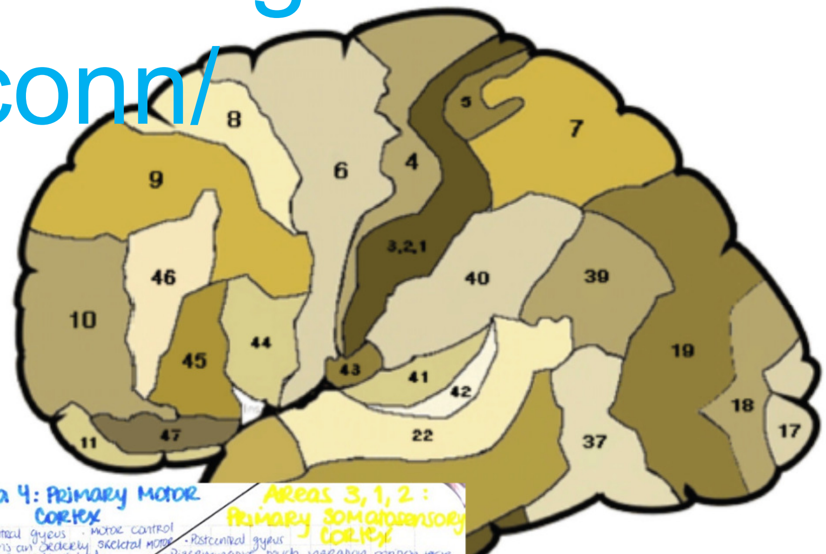


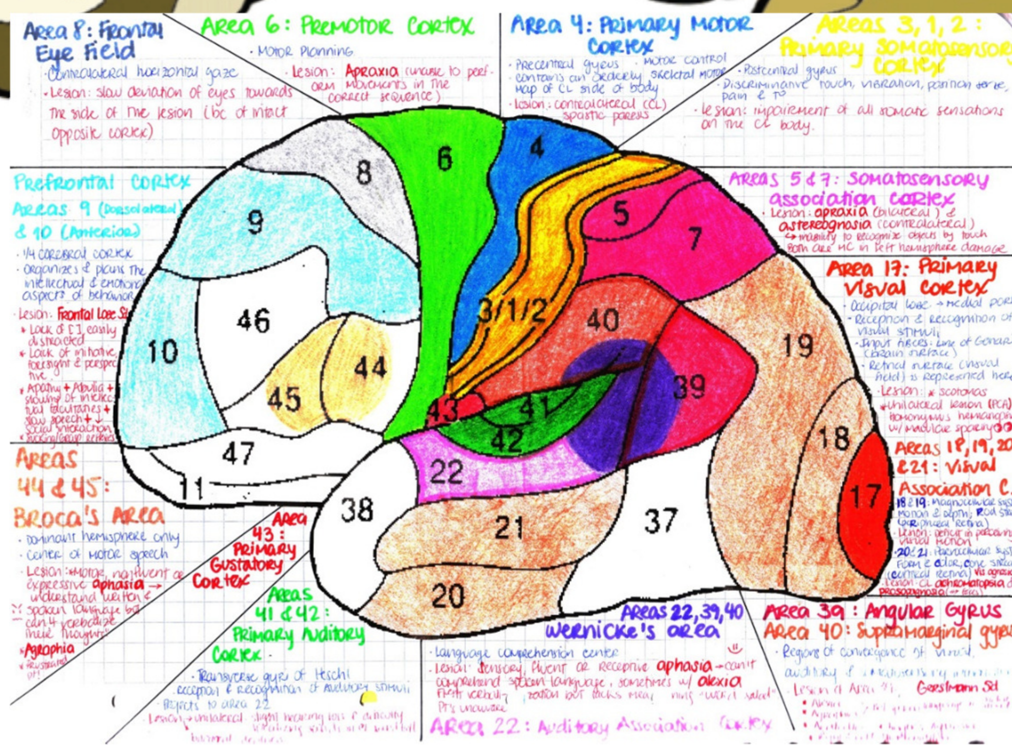
The Least Structured Mammalian Brain is Found in Rodents and Insectivora e.g. in a Mole

Brodmann Areas (Inner and Outer)

http://www.fmriconsulting.com/brodmannconn/







Inappropriate Way to Explain Connectivity…

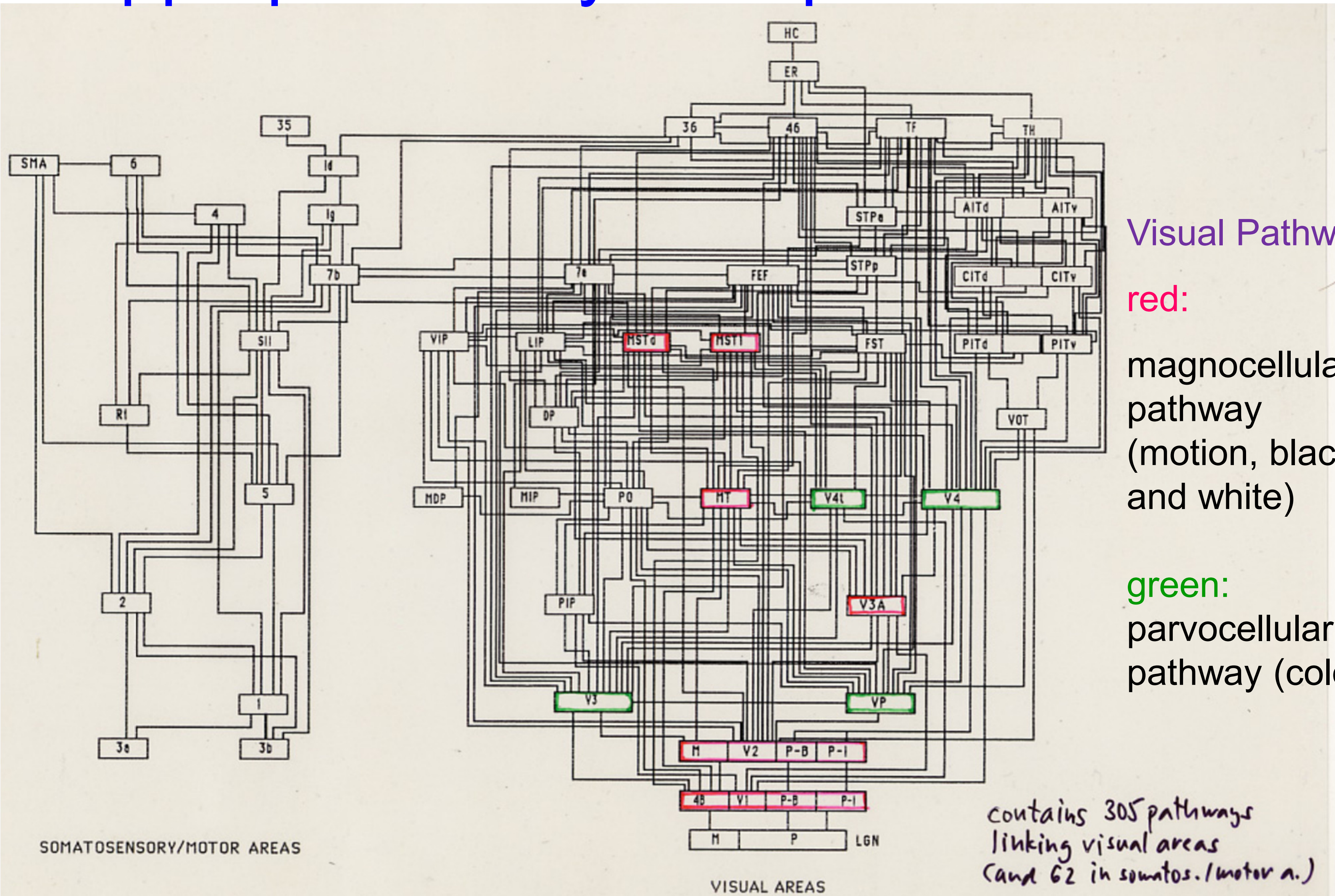


Figure 8. *(See facing page for legend.)*

Van Essen D.C. et al., 1990, Cold Spring Harbor Symp. Quant. Biol., 55: 679-696

Visual Pathways

red:

magnocellular pathway (motion, black and white)

green:
parvocellular pathway (color)

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THIS PANEL IS A SPECULATIVE ATTEMPT TO CLASSIFY BRODMANN AREAS DIFFERENTLY

“Binary Trees of Brodmann Areas” and Beyond Brodmann Areas

- Bit 1: (Left) vs. (Right) Hemisphere
- Bit 2 and 3: (Motor/ Frontal Lobe) (Somatosensory/ Parietal L.)
- Bit 2 and 3: (Auditory/ Temporal L.) (Visual/ Occipital L.)
- Bit 4: (Primary) vs. (Secondary) Sensory projection areas
- Bits 5, 6, 7: subdivisions of visual/ sensory areas
- Sensory Domains: Bits 1 and 7: (Left/ Right) vs. (Bottom/ Top) Extensions, Retinotopy, Spatial Maps
- Bit 8: Temporal encodings: subcortical
- Bit 9: Other modality encodings – Hippocampus (Archi-cortex)/ space navigation, and so on.

Olfactory cortex and Hippocampus (Archi-cortex), Olfacory Bulb (Paleo-cortex), Vestibular Cortex (Part of Temporal lobe), Cortical Projections, Remaining senses: Olfaction, Taste and Touch

What and Where in auditory cortex?

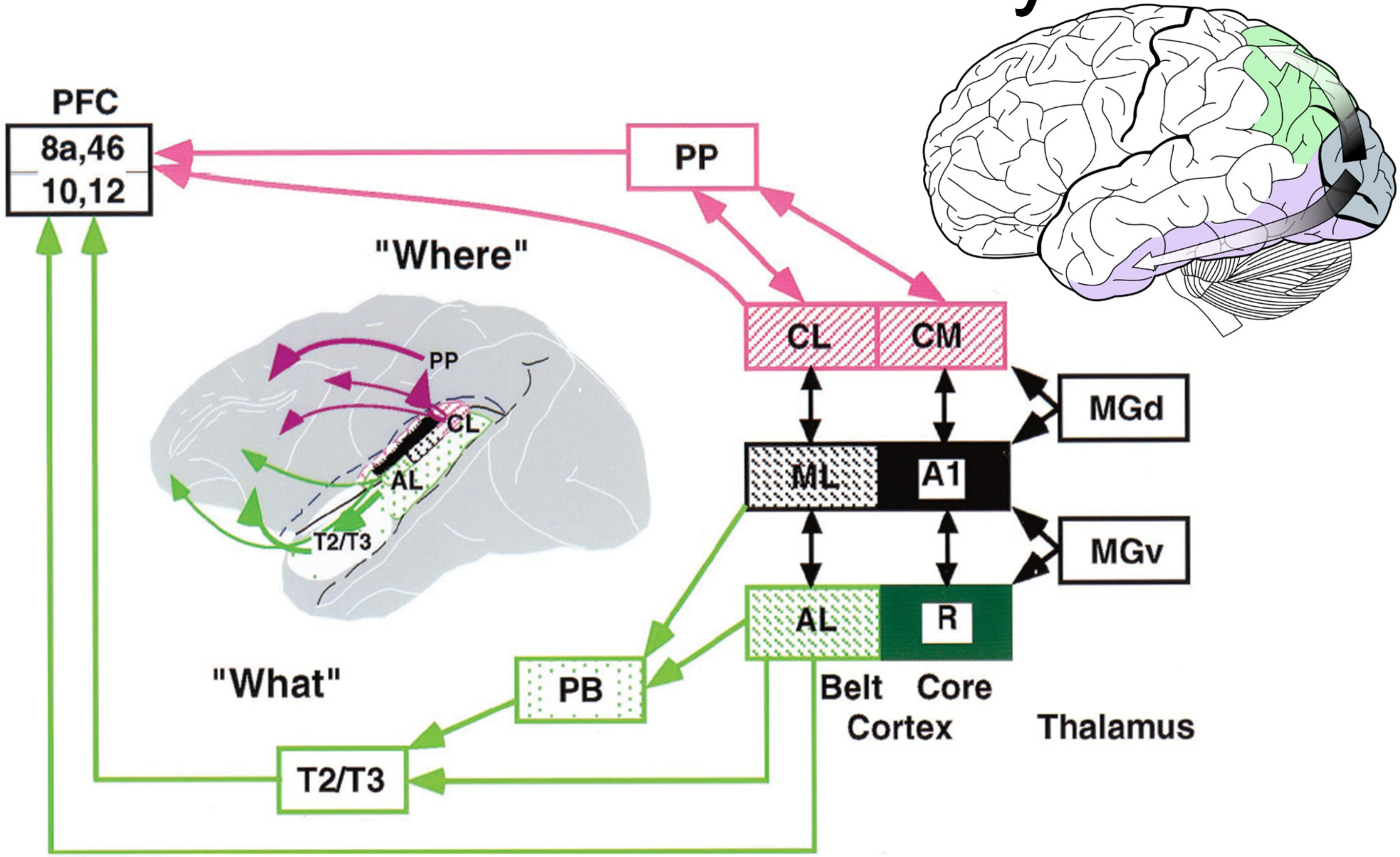
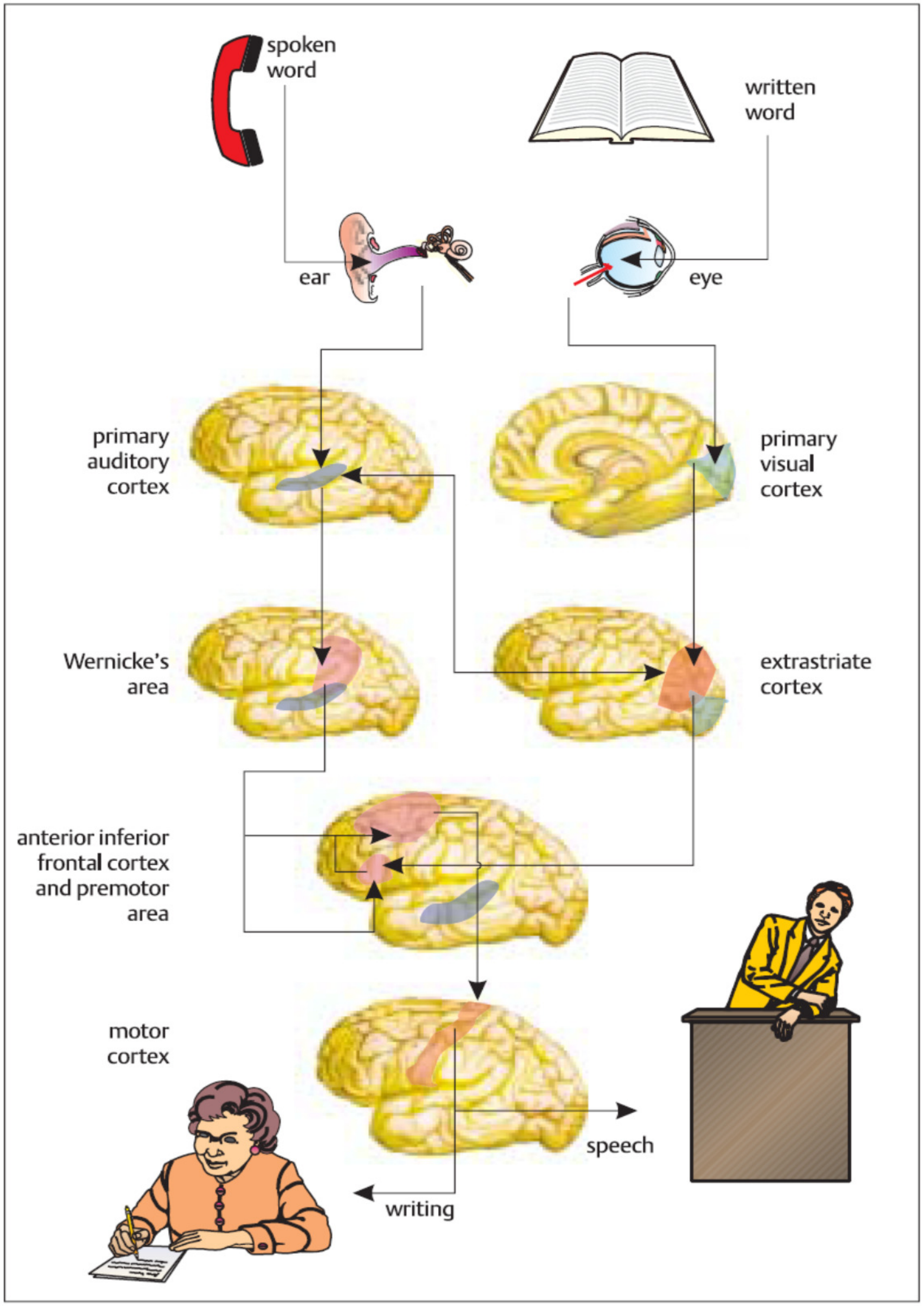
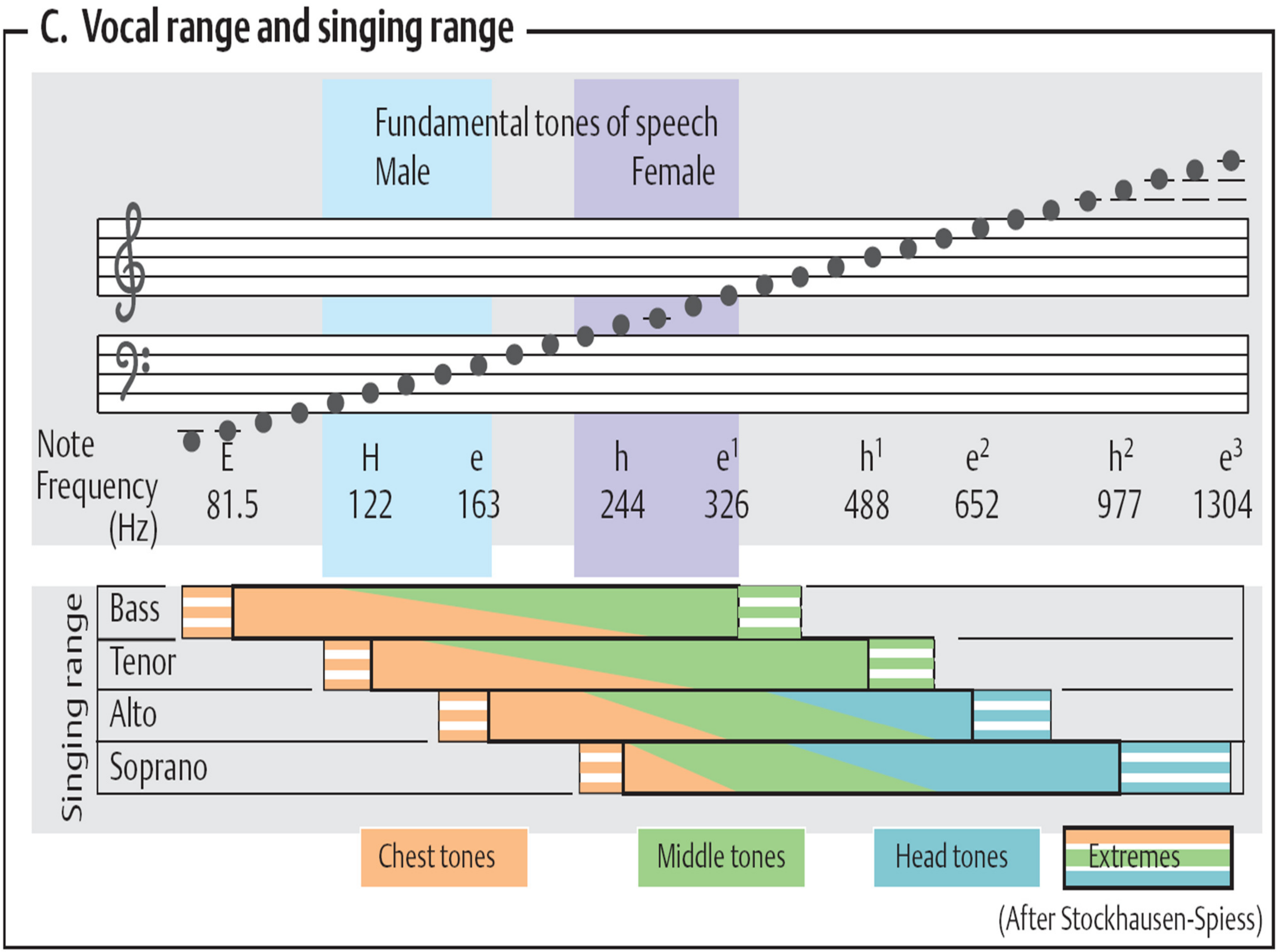


Fig. 6. Schematic flow diagram of "what" and "where" streams in the auditory cortical system of primates. The ventral "what"-stream is shown in green, the dorsal "where"-stream, in red. [Modified and extended from Rauschecker (35); prefrontal connections (PFC) based on Romanski *et al.* (46).] PP, posterior parietal cortex; PB, parabelt cortex; MGd and MGv, dorsal and ventral parts of the MGN.

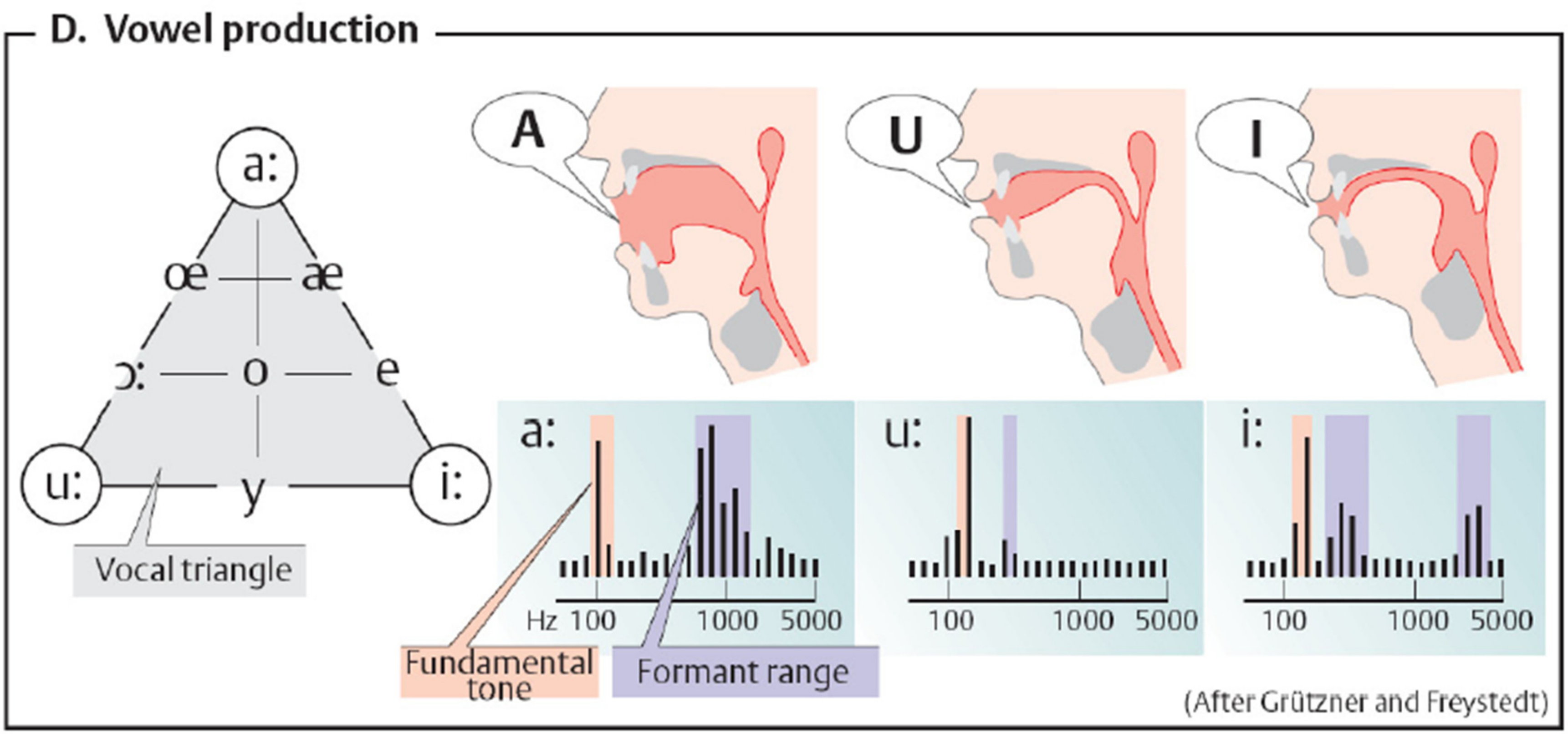


Speech Processing in Cerebral Cortex



Vocal range and singing range + modalities...

Formants of Vowels in Different Languages



Stages of Speech and Language Acquisition

6 mo **Beginning of distinct babbling.**

1 y **Beginning of language understanding, one word utterances.**

1.5 y **Dictionary of 30 to 50 words.**

2 y **Dictionary of 50 to several hundred words. Two word (telegraphic/ short message) speaker.**

2.5 y **Three or more word sentences. Many grammatical errors and idiosyncratic expressions. Good understanding of language.**

3 y **Dictionary of 1000 words.**

4 y **Dictionary of 2000 words. Speech competence close to adults.**

[Kandel, Schwartz, Jessel, Principles of Neural Science, 1991]

EN: babble, CZ: žvatlat, SK: džavotať, GE: plappern,

LAT: balbuties, et cetera…

Comments On Speech Centres

(1) On rare cases of ‘split brain’ patients, it has been demonstrated that lateralization of is a purposeful physiological feature

(2) Sensory speech center deficit (= aphasia) is more devastating than motor aphasia. This is because one does not have a way how to communicate with a patient affected by sensory aphasia.

(3) There are critical developmental periods in native (and foreign) language and speech acquisition.

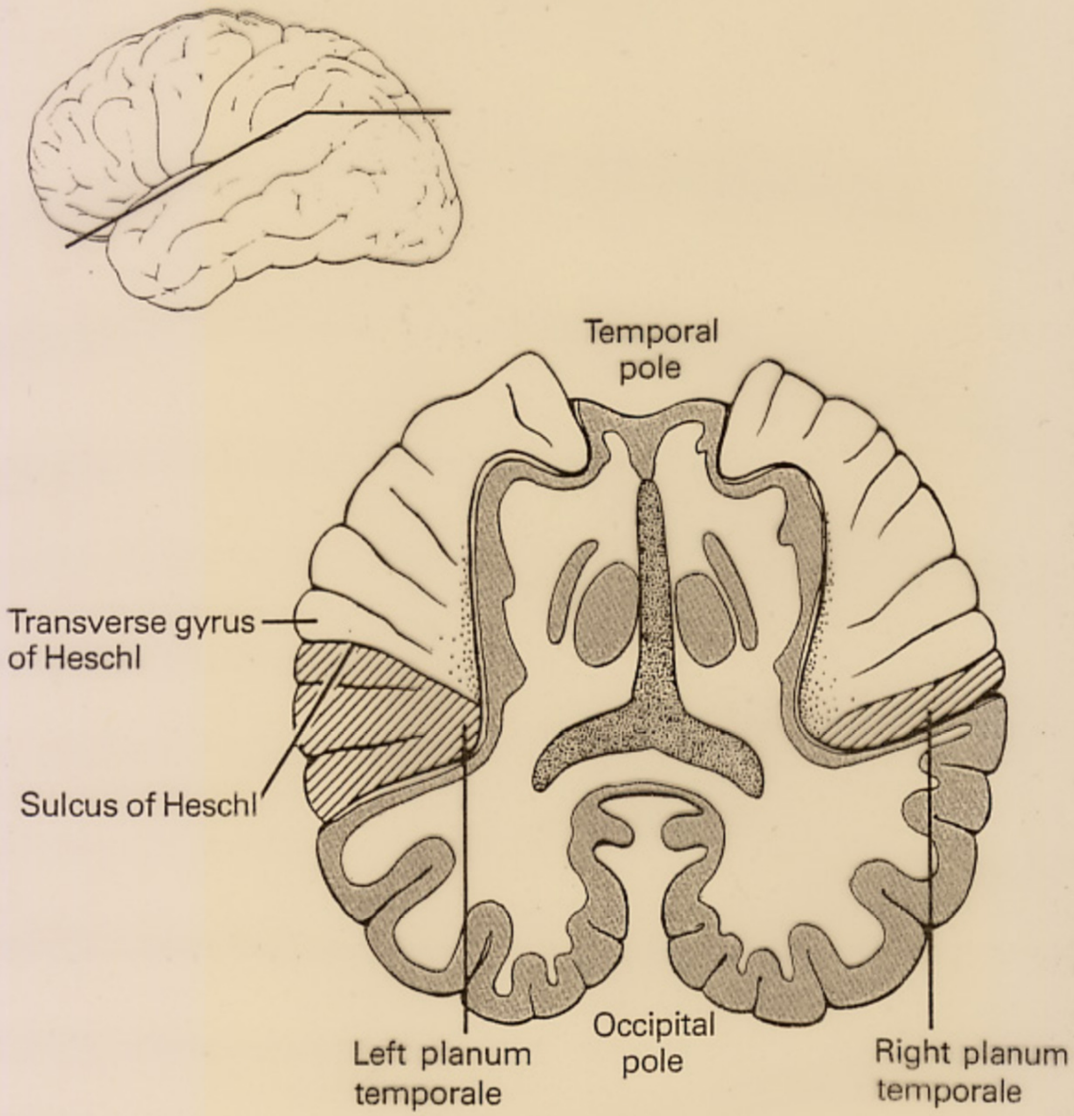


FIGURE 53–8
The planum temporale is larger in the left hemisphere than in the right in the majority of human brains (horizontal section in the plane of the Sylvian fissure). (Adapted from Geschwind and Levitsky, 1968.)

TABLE 53–2. Linguistic Dominance and Handedness

	Dominant hemisphere (%)		
Handedness	Left	Right	Both
Left or mixed handed	70	15	15
Right handed	96	4	0

(Data from Rasmussen and Milner, 1977.)

All Conscious Mental Processes Reside in Cerebral Cortex

Psycho-Physical and Electro-Encephalo-Graphic Responses of Infants and Small Children

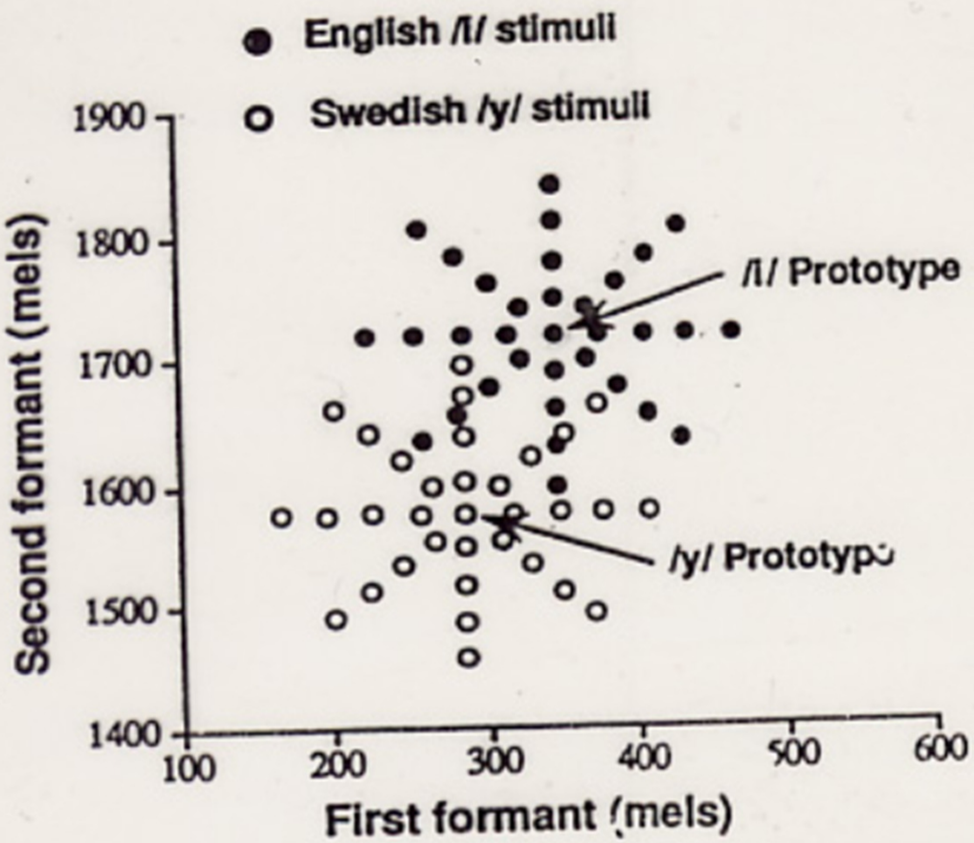


Fig. 1. Six-month-old infants from America and Sweden were tested with two sets of vowel stimuli, American English /i/ and Swedish /y/. Each set included an exceptionally good instance of the vowel (the prototype) and 32 variants that formed four rings (eight stimuli each) around the prototype (*8*).

Prototypes of vowels and synthetic vowels in formant space
[P. Kuhl et al, 1992]

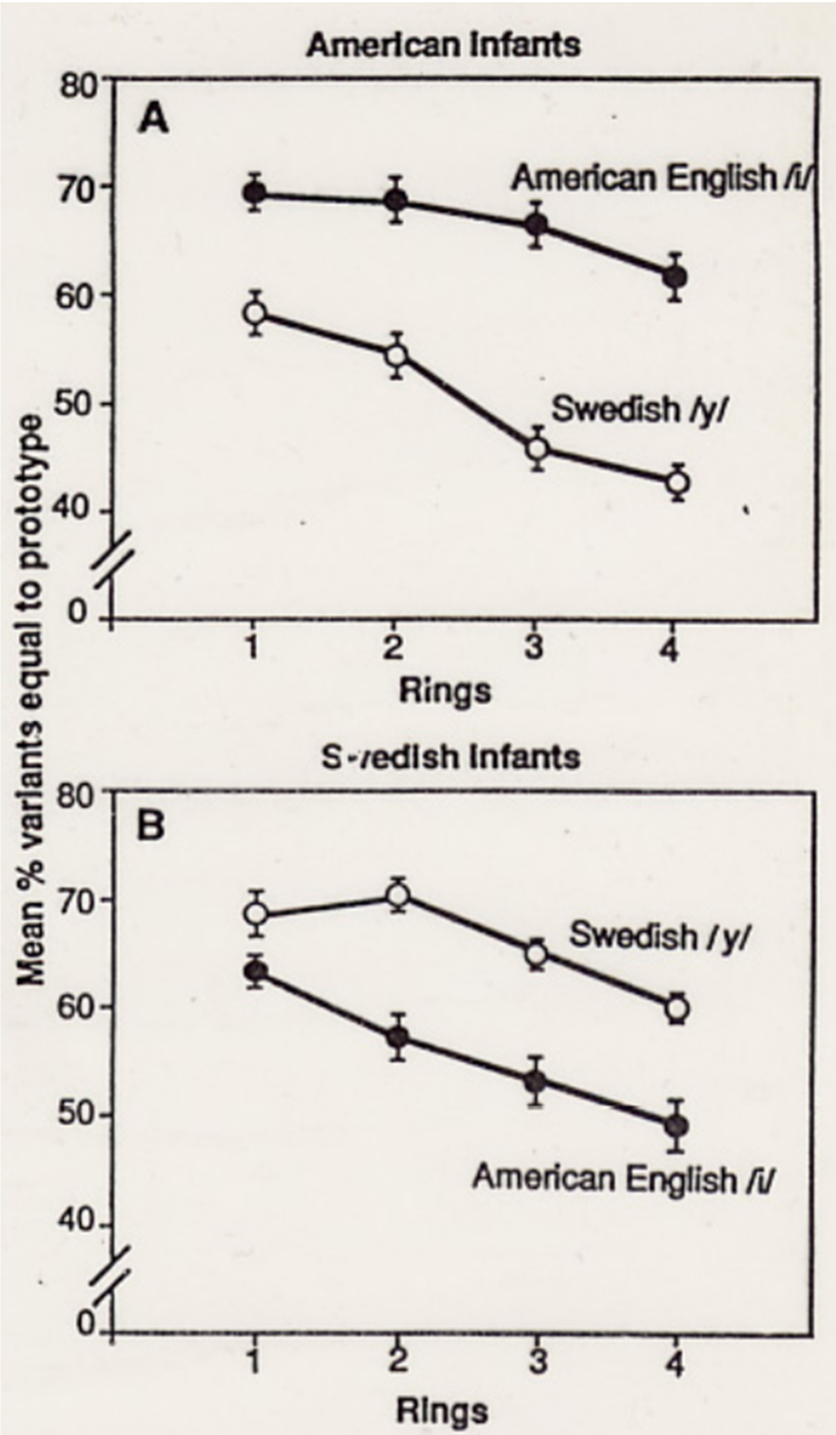
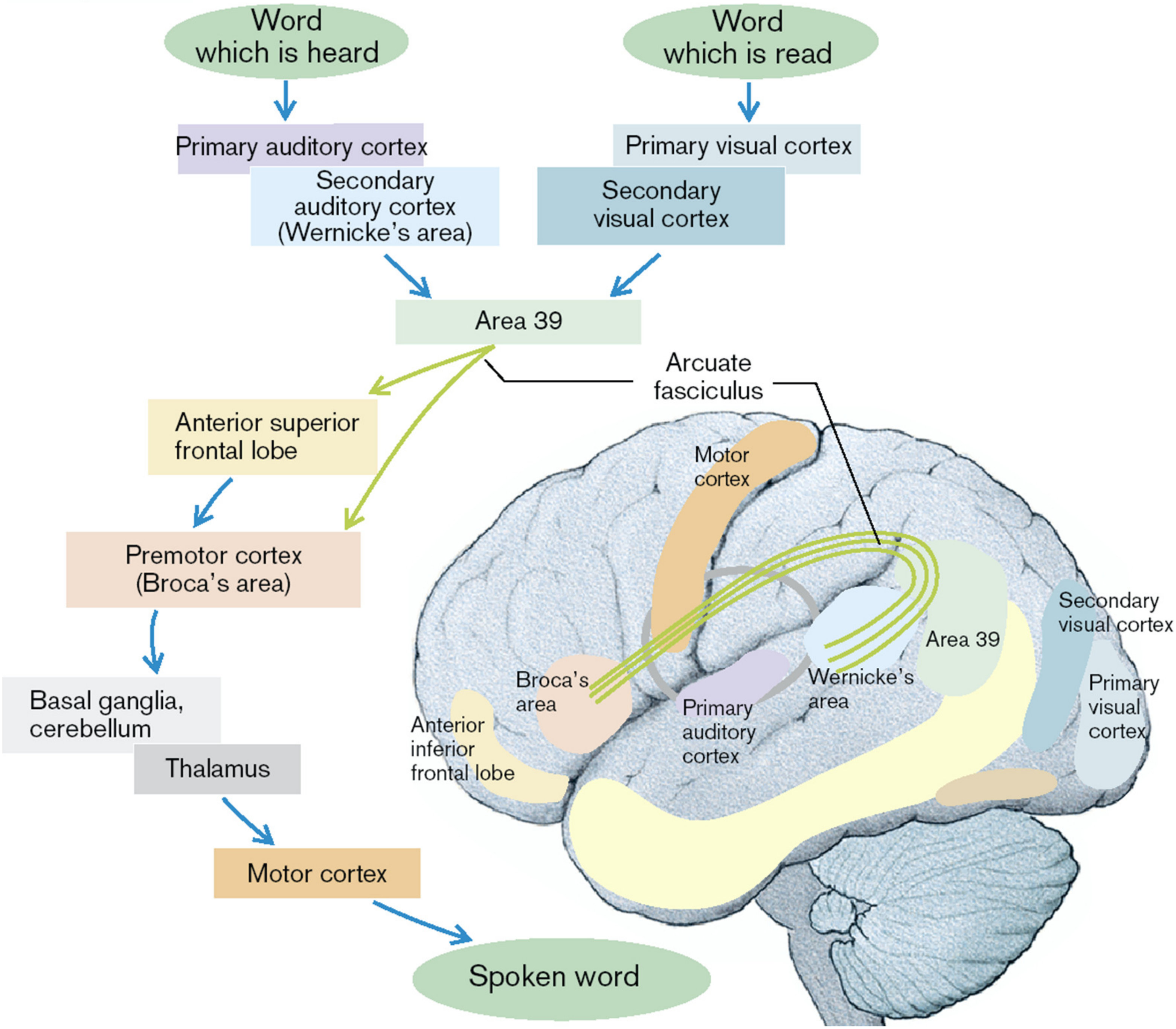


Fig. 2. Results showing an effect of language experience on young infants' perception of speech. Two groups of 6-month-old infants, (**A**) American and (**B**) Swedish, were tested with two different vowel prototypes, American English /i/ and Swedish /y/. The mean percentage of trials in which infants equated variants on each of the four rings to the prototype is plotted. Infants from both countries produced a stronger magnet effect (equated variants to the prototype more often) for the native-language vowel prototype when compared to the foreign-language vowel prototype. (Error bars = standard error.)

Psycho-physical responses of 6 month old infants to vowels of native and foreign language

[P. Kuhl et al, 1992]

A. Aphasias



Word which is heard
Primary auditory cortex
Secondary auditory cortex (Wernicke's area)
Word which is read
Primary visual cortex
Secondary visual cortex
Area 39
Arcuate fasciculus
Anterior superior frontal lobe
Premotor cortex (Broca's area)
Basal ganglia, cerebellum
Thalamus
Motor cortex
Spoken word
Motor cortex
Broca's area
Anterior inferior frontal lobe
Primary auditory cortex
Wernicke's area
Area 39
Secondary visual cortex
Primary visual cortex

Type	Spontaneous speech	Repetition of words	Language comprehension	Finding words
Broca's aphasia	abnormal	abnormal	normal	impaired
Wernicke's aphasia	fluent (at times logorrhea, paraphasia, neologisms)	abnormal	impaired	impaired
Conduction aphasia	fluent, but paraphasic	markedly impaired	normal	abnormal, paraphasic
Global aphasia	abnormal	abnormal	abnormal	abnormal
Anomic aphasia	fluent	normal, but anomic	normal	impaired
Achromatic aphasia	fluent	normal, but anomic	normal	impaired
Motor transcortical aphasia	abnormal	normal	normal	abnormal
Sensory transcortical aphasia	fluent	fluent	abnormal	abnormal
Subcortical aphasia	fluent	normal	abnormal (transient)	abnormal (transient)

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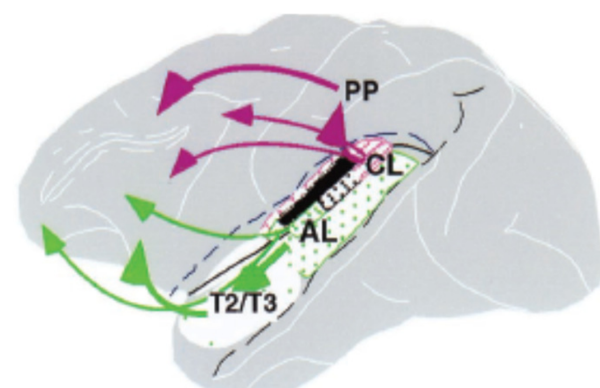
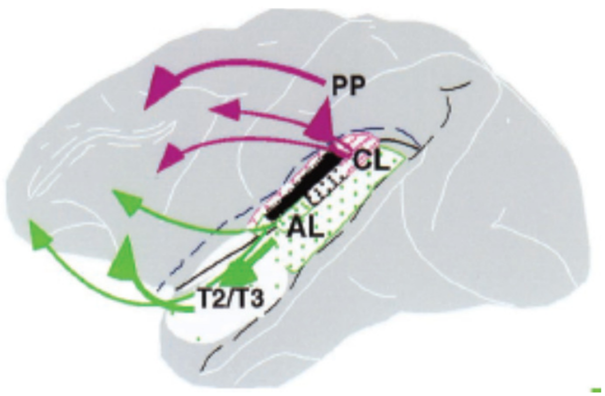


Thanks for your attention

CTU FEE



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END
OF THE LECTURE

(Outline) Conclusions – Binaural hearing

1. Introduction: coincidence detectors are part of the circuit
2. Hypothetically it is possible that coincidence detectors are at different processing stages
3. Several models are discussed: with and without synaptic mechanisms, with and without cochlear mechanics, and other variants
4. Outputs of all models are evaluated by the ideal observer
5. Questions addressed/ open questions
6. Example: Can modeling phase information improve our description/ understanding of MSO (= low frequency encoding) mechanisms?

Group: Audiology, Acoustics and Computational Neuroscience, CTU and 1stMF CUni (year 2015)