

Brain Imaging of auditory function

Maria Chait

Who am I?

- I do (mostly) MEG functional brain imaging of auditory processing.
- Now, I am at the EAR Institute, University College London
&
Equipe Audition, LPP, Paris 5, ENS
- PhD from the University of Maryland, USA
 - Cognitive Neuroscience of Language Laboratory
 - Computational Sensory Motor Systems Laboratory

Outline:

- Introduction to brain imaging techniques.
- Spatial processing
- Pitch and melody
- Attention
- Change detection and MMN
- Speech
- Brain asymmetry

Some Slides/Images are taken from:

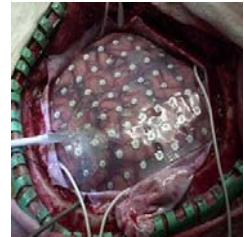
- <http://psychology.uwo.ca/fmri4newbies/>
- David Poeppel
- Colin Phillips
- Wikipedia
- Istvan Winkler
- Gazzaniga et al. (eds) 'Cognitive Neuroscience'

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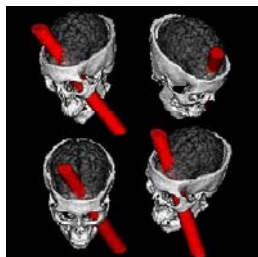
functional brain mapping in humans

- Subdural recording



functional brain mapping in humans

- Subdural recording
- Lesion study

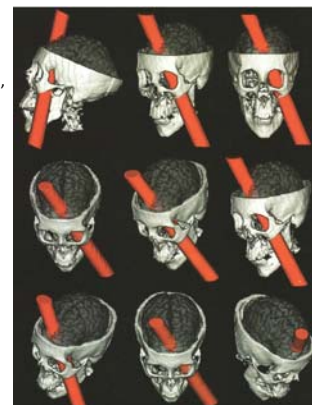


Phineas Gage, 1848

Before: responsible, well-mannered, well-liked, efficient worker, pious

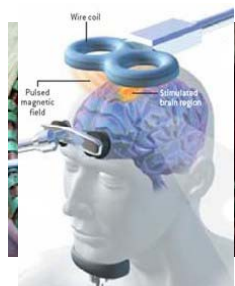
After: capricious, impulsive, irreverent, hypersexual

Damage involved VMPFC



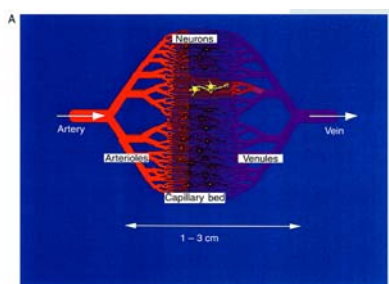
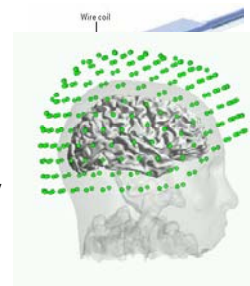
functional brain mapping in humans

- Subdural recording
- Lesion study
- Trans-cranial magnetic stimulation (TMS)
Non-invasive method to study brain circuitry and connectivity. Localized neural excitation is caused by weak electric currents induced in the tissue by rapidly changing magnetic fields.



functional brain mapping in humans

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Non-invasive method to study brain circuitry and connectivity. Localized neural excitation is caused by weak electric currents induced in the tissue by rapidly changing magnetic fields.
- Non invasive functional brain imaging methods

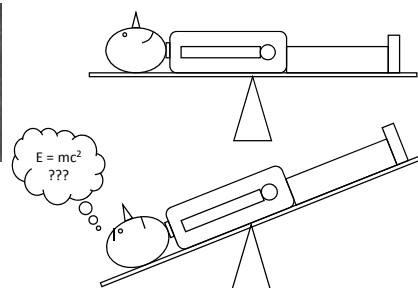


- Active neurons release the neurotransmitter glutamate
- Glutamate opens NMDA receptors on other neurons which allows calcium ions in
- Calcium activates the production of nitric oxide
- Nitric oxide diffuses out and dilates smooth muscle surrounding local arterioles
- This allows more blood into the local capillaries
- More oxygen and glucose reaches the neurons

The First "Brain Imaging Experiment"



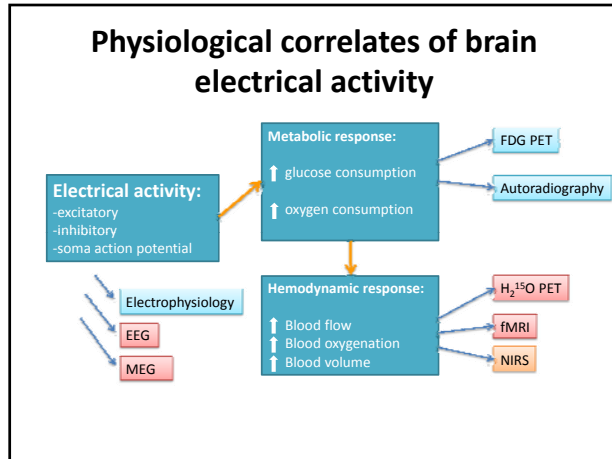
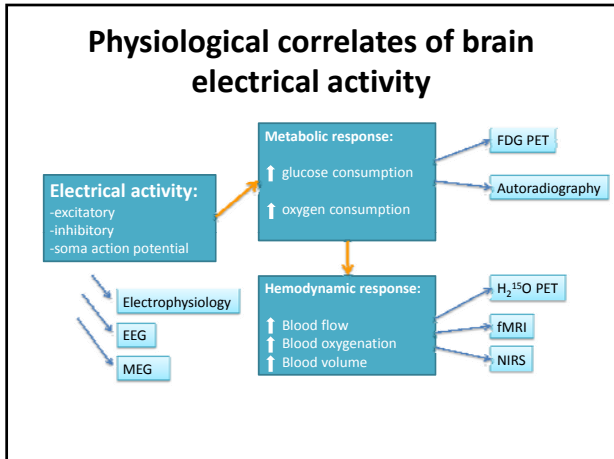
Angelo Mosso
Italian physiologist
(1846-1910)



"[In Mosso's experiments] the subject to be observed lay on a delicately balanced table which could tip downward either at the head or at the foot if the weight of either end were increased. The moment emotional or intellectual activity began in the subject, down went the balance at the head-end, in consequence of the redistribution of blood in his system."

— William James, *Principles of Psychology* (1890)

From <http://psychology.uwo.ca/fmri4newbies/>



Positron Emission Tomography (PET)

Positron Emission Tomography (PET)

The system detects coincident pairs of gamma rays emitted by annihilation of a positron-emitting radioisotope, which is introduced into the body on a metabolically active molecule.

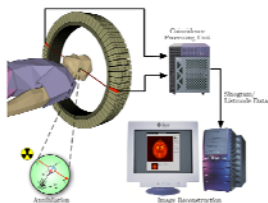
Positron Emission Tomography (PET)

Advantages:

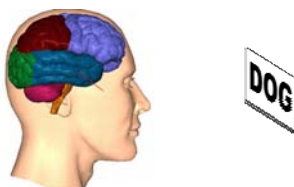
- Good spatial resolution
- Silent

Limitations:

- Moderately Invasive (requires injection of radio nuclides)
- high costs of radio nuclides production.
- Short half life of radio nuclides.
- Poor temporal resolution (requires block design)



Why Temporal Resolution is important: An example from the Lexical Decision task



Required operations:

- Visual registration
- Grapheme-to-phoneme conversion
- Lexical search
- Remembering the task
- Motor response

< 900 ms
distributed processing in
neural networks

PET methodology

1. Block design

Tasks are run in blocks of 30-60 seconds duration. During each block, the same experimental task must be executed for the entire block duration.

The different experimental blocks are chosen to be in a "hierarchical" or "nested" relationship.

2. Paired-image subtraction

PET images are collected during the execution of blocks and subtracted from one another.

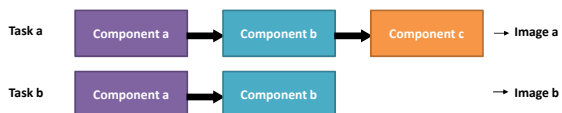
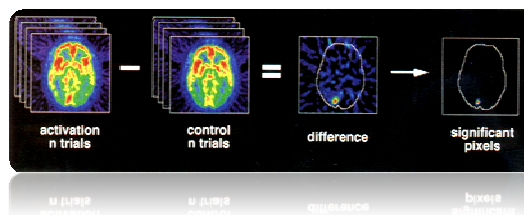


Image a MINUS Image b = difference image (pixel-by-pixel subtraction)
Local activation in difference image is responsible for Component c



From <http://psychology.uwo.ca/fmri4newbies/>

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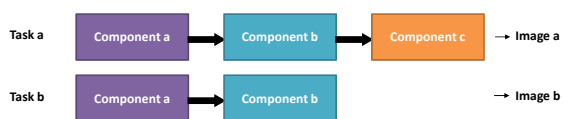


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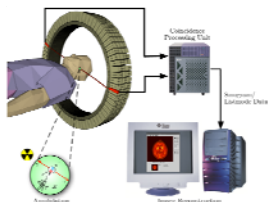
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Near infrared spectroscopy (NIRS)

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The primary absorbers in tissue at near-infrared wavelengths:

- Water
- **oxygenated haemoglobin (HbO)**
- **deoxygenated haemoglobin (Hb)**

transmission and absorption of NIR light in brain tissues contains information about haemoglobin concentration changes and oxygen saturation.



Near infrared spectroscopy (NIRS)

Advantages:

- Non invasive
- can be used on infants
- much more portable than fMRI machines

Limitations:

- Works at only centimetre depths (cortical).
- Poor temporal resolution.

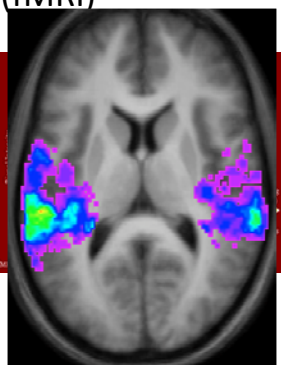


Functional magnetic resonance imaging (fMRI)

A method of observing which areas of the brain are active at any given time, based on measuring the degree of magnetization of a haemoglobin in response to an applied magnetic field.

the difference in magnetization between oxygenated haemoglobin and deoxygenated haemoglobin causes magnetic signal variation which is detectable with an MRI scanner.

BOLD=Blood Oxygenation Level Dependent RESPONSE



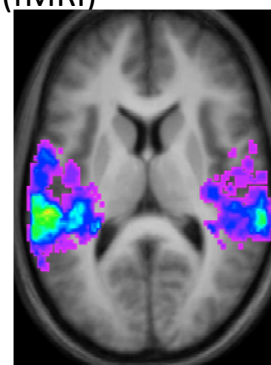
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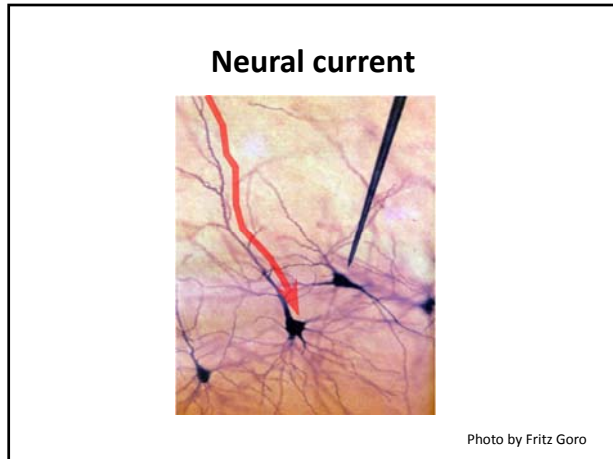
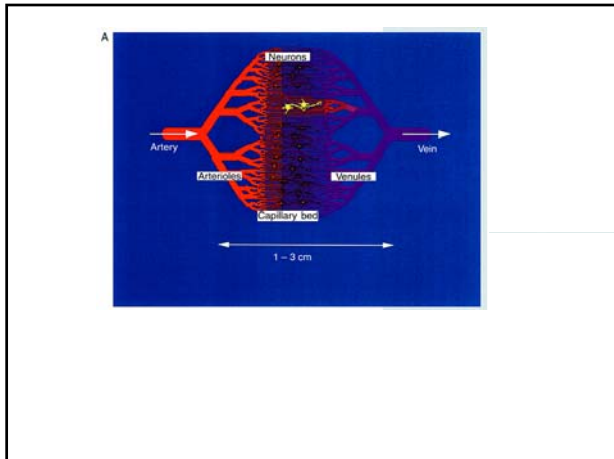
Advantages:

- Non invasive
- Spatial resolution in the region of 3-6 millimetres.

Limitations:

- Very noisy.
- Poor temporal resolution.
- Block design is usually used.



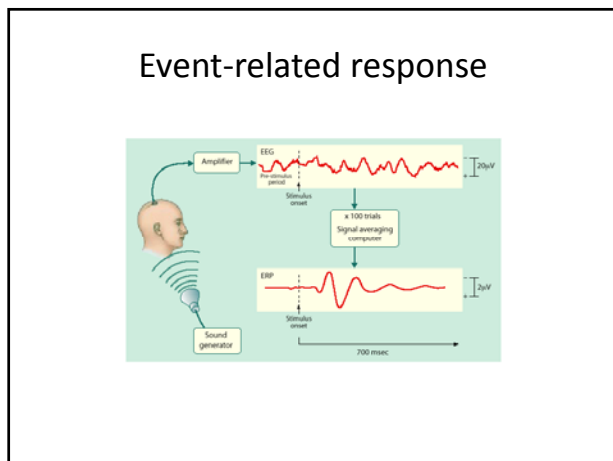


Electroencephalography (EEG)

neurophysiologic measurement of the electrical activity of the brain by recording from electrodes placed on the scalp. The resulting represent a summation of post-synaptic potentials from a large number of neurons.

The diagram shows a person's head from the side, wearing a cap with numerous electrodes. A small circuit diagram is overlaid on the head, showing a voltage source (V) and a current source (I) connected to the electrodes. A smiley face icon is also present.

An evoked potential (or "evoked response") is an electrical potential recorded following presentation of a stimulus (as opposed to spontaneous) and is computed by averaging over stimulus presentations.



Electroencephalography (EEG)

Advantages:

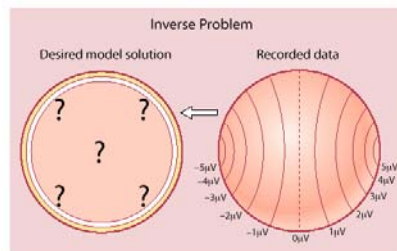
- Non invasive and passive.
- Excellent temporal resolution (direct measure of neural activity)
- Relatively cheap to set-up

Limitations:

- Poor spatial resolution (inverse problem is ambiguous)



Inverse Problem



Electroencephalography (EEG)

Advantages:

- Non invasive and passive.
- Excellent temporal resolution (direct measure of neural activity)
- Relatively cheap to set-up

Limitations:

- Poor spatial resolution (inverse problem is ambiguous)
- 'blind' to tangential currents
- Visible activity only for synchronous activation of many (~ 10^4 ~ 10^6) neurons



Magnetoencephalography (MEG)

measure the magnetic fields produced by electrical activity in the brain via extremely sensitive devices such as superconducting quantum interference devices (SQUIDS).

signals derive from the net effect of ionic currents flowing in the dendrites of neurons during synaptic transmission.

SQUID detectors measure brain magnetic fields around 100 billion times weaker than earth's steady magnetic field



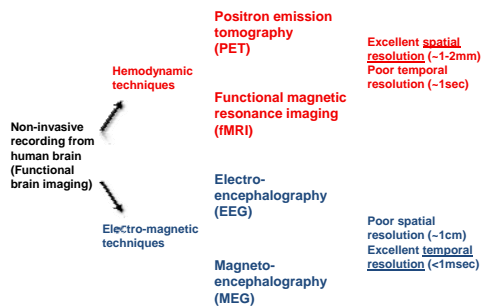
Magnetoencephalography (MEG)

Advantages:

- Non-invasive and passive.
- Excellent temporal resolution (direct measure of neural activity)
- Auditory Cortex is in the 'Fovea' of MEG
- Spatial resolution better than EEG.

Limitations:

- Poor spatial resolution (inverse problem is ambiguous)
- 'blind' to perpendicular currents
- Visible activity only for synchronous activation of many ($\sim 10^4 \sim 10^6$) neurons



Why Temporal Resolution is important: An example from the Lexical Decision task

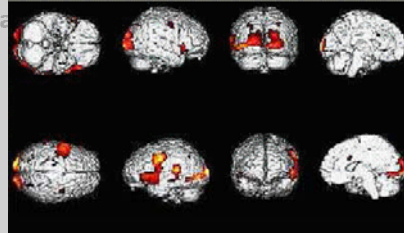


Required operations:

- Visual registration
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- Lexical search
- Remembering the task
- Motor response

< 900 ms
distributed processing in neural networks

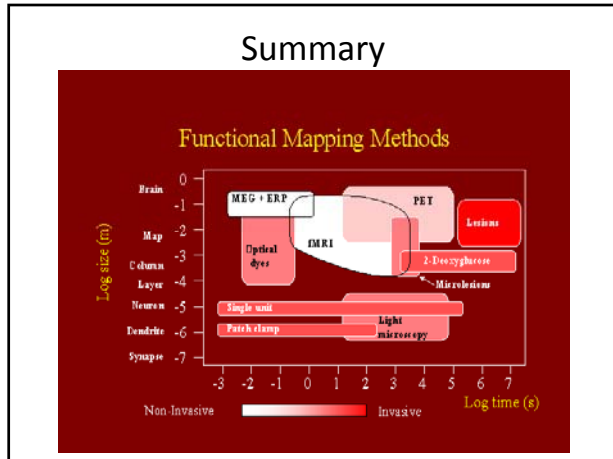
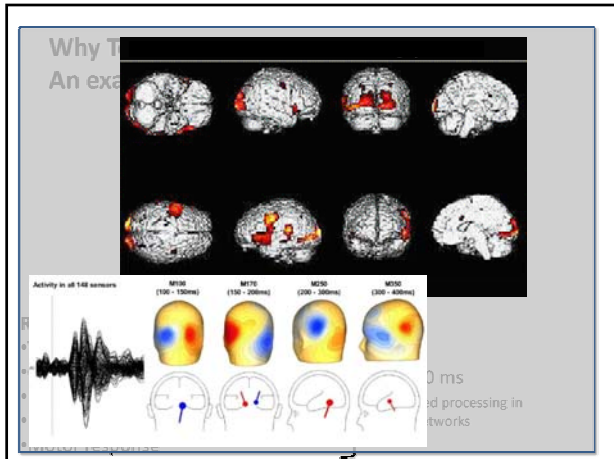
Why T... An exa...



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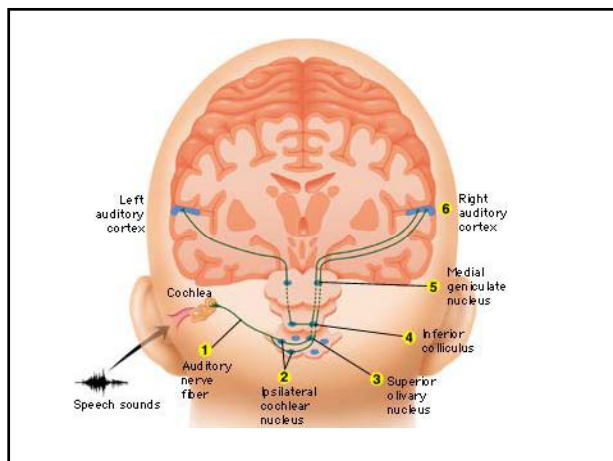
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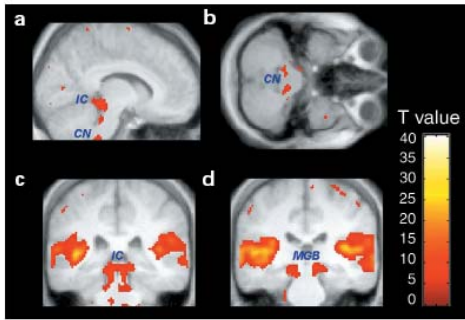
brain imaging techniques - Summary

- Different functional brain imaging techniques have specific limitations (e.g. what is measured, how results should be interpreted, etc)
- require different experimental design
- Are designed to answer different questions about processing (e.g. 'where' vs. 'when')

The auditory pathway

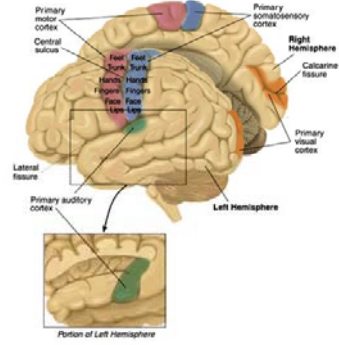


Activation of structures in the ascending auditory pathway with sound stimuli:

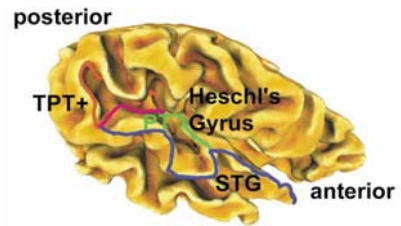
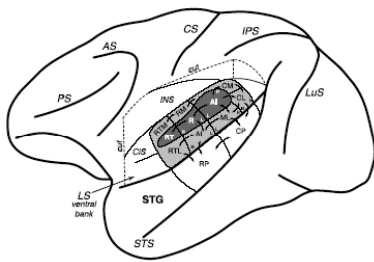


Griffiths et al, 2001

► Lateral View of the Left Side of a Human Brain



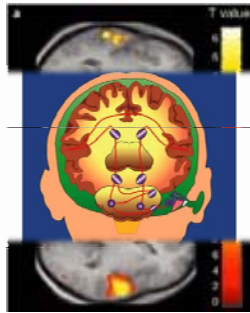
From animal models:



(Figure from Ratnanather et al, NeuroImage 2003, vol 20[1])

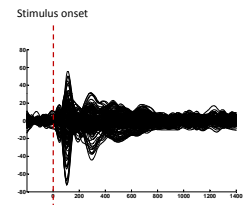
MEG vs. fMRI data interpretation

- If brain area X is the first, in a hypothesized pathway, to be activated by a stimulus feature, then it is hypothesized that this area is involved in extracting that feature.
- If activation in area X is modulated by change in a particular feature, then it is involved in processing that feature.



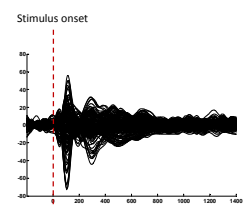
MEG vs. fMRI data interpretation

- The activation pattern, consisting of increases in activation at different latencies, reflects the sequential operation of cortical systems related to analyzing the stimulus
- Cortical processing can be studied by investigating which stimulus features affect the latency or amplitude of these responses.



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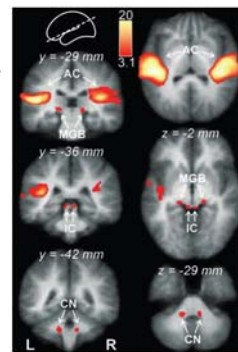
- Introduction to brain imaging techniques.
- **Spatial processing**
- Pitch and melody
- Attention
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- Speech
- Brain asymmetry

Spatial processing

Contrast between all sound conditions and silence

- fMRI stimuli:
- Silence
 - Left ear noise bursts
 - Right ear noise bursts
 - Center noise bursts
 - Moving noise bursts

Spatial percept manipulated by ITD



Krumbholz et al, 2005

Spatial processing

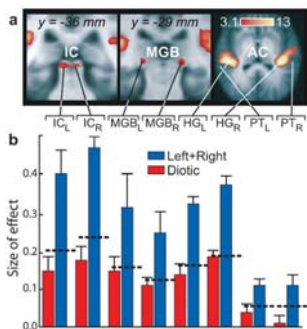
Binaural difference contrast:
Center minus (left+right)
(all referred to silence)

Binaural interaction in IC, MGB and PAC

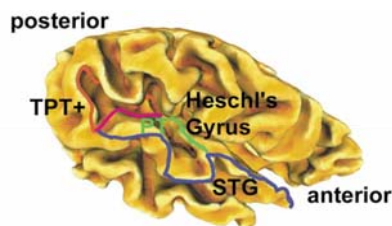
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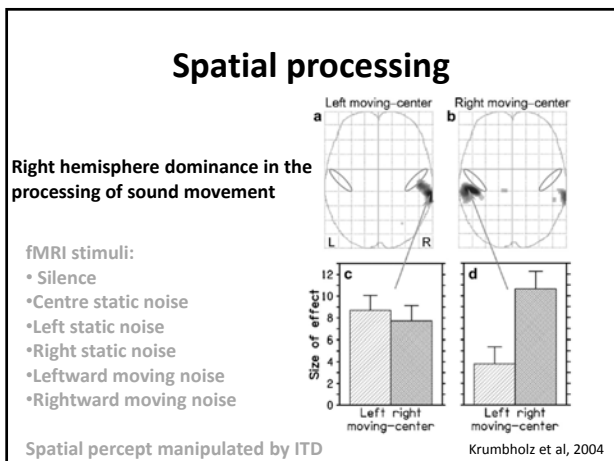
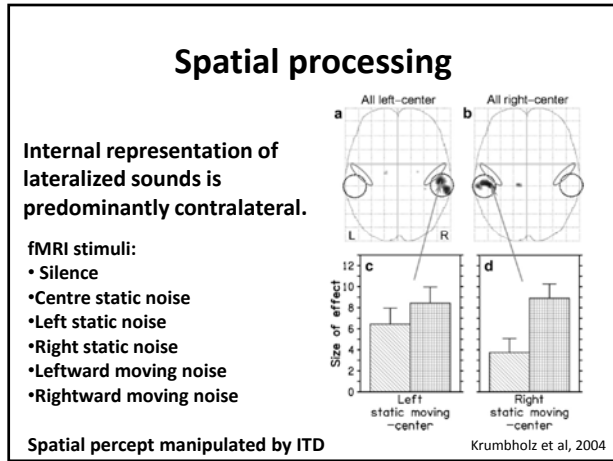
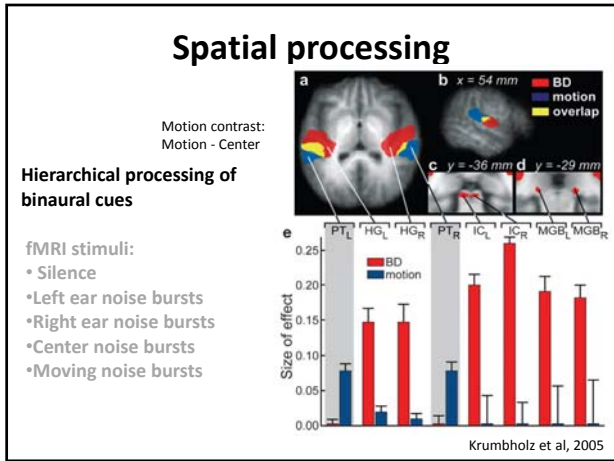
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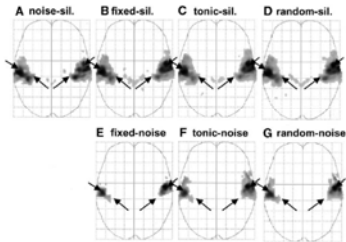
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Pitch Processing

Contrasts:



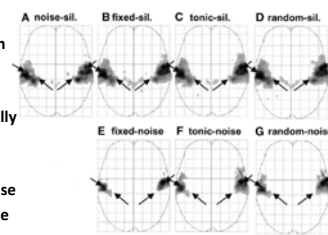
fMRI stimuli:

- Silence
- Noise
- Fixed Pitch (IRN)
- Changing pitch (tonic)
- Changing pitch (random)

Patterson et al, 2002

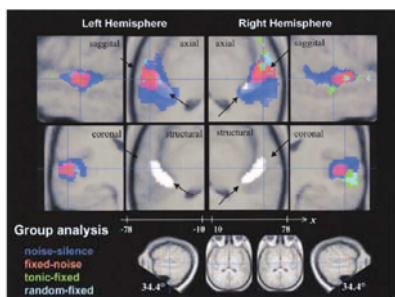
Pitch Processing

There are a number of centers in auditory cortex (HG and PT) that process all stimuli coming up from subcortical structures in both hemispheres, and one of these regions in lateral HG is differentially active in the presence of pitch.



All of the regions activated by noise were activated to the same degree by sounds with pitch.

Patterson et al, 2002

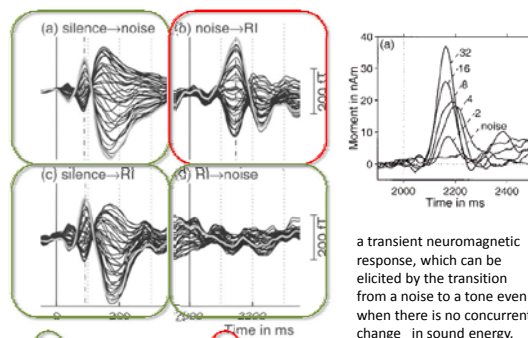


fMRI stimuli:

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sounds with pitch produced more activation than those without pitch only in the lateral half of Heschl's gyrus (HG).

Patterson et al, 2002



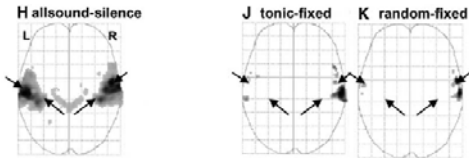
a transient neuromagnetic response, which can be elicited by the transition from a noise to a tone even when there is no concurrent change in sound energy.

MEG stimuli:



Krumbholz et al, 2003

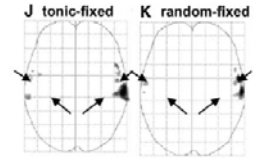
Processing of melody



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Patterson et al, 2002

Processing of melody

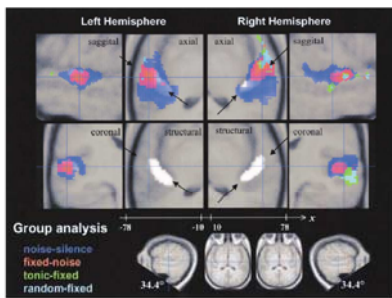


More later

Both contrasts reveal differential activation to melody in STG and PP, but in this case, the activation is asymmetric (more activity in the right hemisphere)

Melody produced the same level of activity as fixed pitch in HG. This suggests that HG is involved in short-term rather than longer-term pitch processing.

Patterson et al, 2002



- fMRI stimuli:
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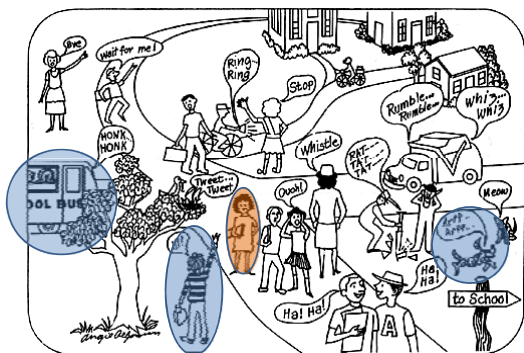
Hierarchy of pitch processing in auditory cortex

Patterson et al, 2002

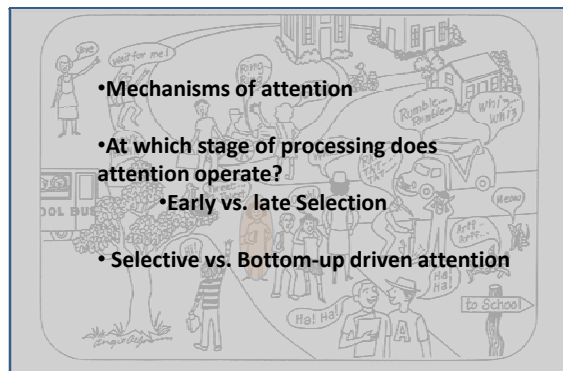
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Attention

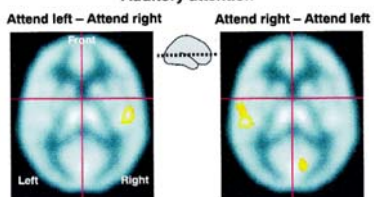


Attention



Selective attention

Auditory attention

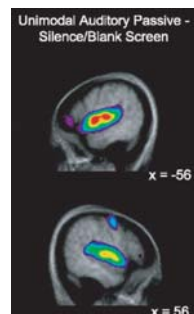


PET stimuli:

- 3 concurrent streams: Left Ear, Right Ear, Visual
- Task:
 - attend left ear (detect deviant tones)
 - attend right ear
 - attend visual

Alho et al, 1999

Selective attention



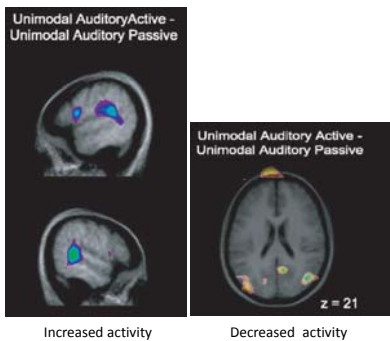
fMRI stimuli:

- Melodies and shapes.
- silence + blank screen
- Unimodal Aud passive
- Unimodal Aud active
- Unimodal Vis passive
- Unimodal Vis active
- Bimodal passive
- Bimodal Aud active
- Bimodal Vis active

Johnson & Zatorre, 2005

Selective attention

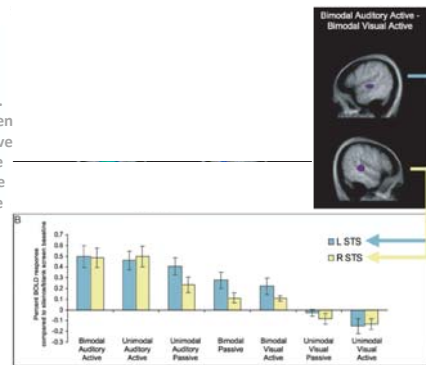
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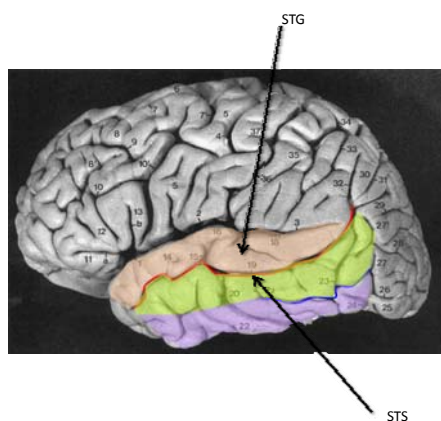
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fMRI stimuli:
 Melodies and shapes.
 • silence + blank screen
 • Unimodal Aud passive
 • Unimodal Aud active
 • Unimodal Vis passive
 • Unimodal Aud active
 • Bimodal passive
 • Bimodal Aud active
 • Bimodal Vis active



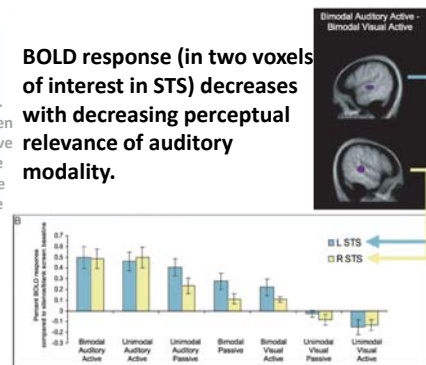
Johnson & Zatorre, 2005



Selective attention

fMRI stimuli:
 Melodies and shapes.
 • silence + blank screen
 • Unimodal Aud passive
 • Unimodal Aud active
 • Unimodal Vis passive
 • Unimodal Aud active
 • Bimodal passive
 • Bimodal Aud active
 • Bimodal Vis active

BOLD response (in two voxels of interest in STS) decreases with decreasing perceptual relevance of auditory modality.



Johnson & Zatorre, 2005

Temporal properties of auditory attention

Example from EEG:

Attended
 Unattended

Alain & Izenberg, 2003

Temporal properties of auditory attention

MEG stimuli:
Sequences of tones in left and right ear.

Task:
•Attend left
•Attend right

Attention verified by measuring detection-task performance

Early selection mechanism for auditory attention ?

Woldorff et al, 1993

Temporal properties of auditory attention

An example from Vision:

MEG stimuli:
Sequences of tones in left and right ear.

Task:
•Attend left
•Attend right

Attention verified by measuring detection-task performance

Cortico-cortical feedback

Early selection mechanism for auditory attention ?

Super et al, 2001

Temporal properties of auditory attention

MEG stimuli:
Sequences of tones in left and right ear.

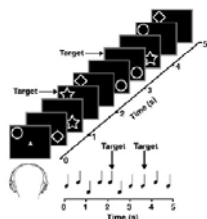
Task:
•Attend left
•Attend right

Attention verified by measuring detection-task performance

Early selection mechanism for auditory attention ?

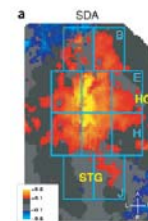
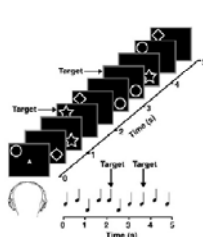
Woldorff et al, 1993

Attentional modulation of human auditory cortex



Petkov et al, 2004

Attentional modulation of human auditory cortex

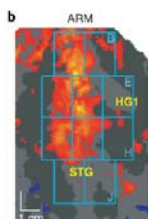
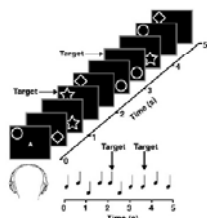


- Maximal in STG
- Enhanced in contralateral hemisphere
- Influenced by sound frequency (tonotopic organization)

Stimulus-dependent activation
 Visual attention w-auditory signal minus
 Visual attention without auditory signals

Petkov et al, 2004

Attentional modulation of human auditory cortex

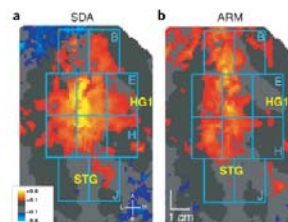


Attention-related activation

Auditory attention minus
 Visual attention

Petkov et al, 2004

Attentional modulation of human auditory cortex

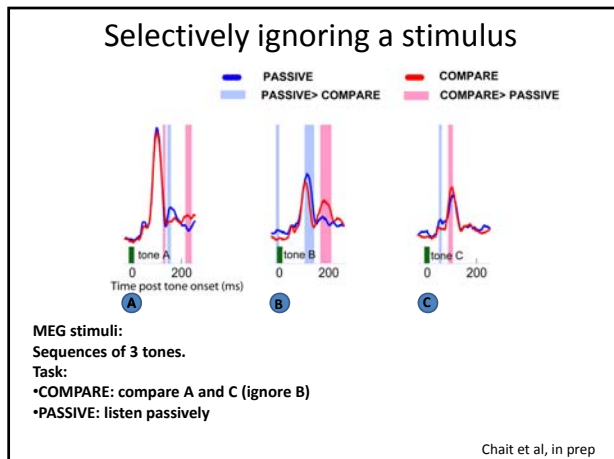


Stimulus-dependent activation

Attention-related activation

Auditory attention does not just amplify neural responses

Petkov et al, 2004



Attention

- Enhances relevant stimuli
- Suppresses irrelevant stimuli
- Changes *how* stimuli are processed.

Krumholz study here

Attention Changes sound representation in auditory cortex

fMRI stimuli:
FM sweeps.

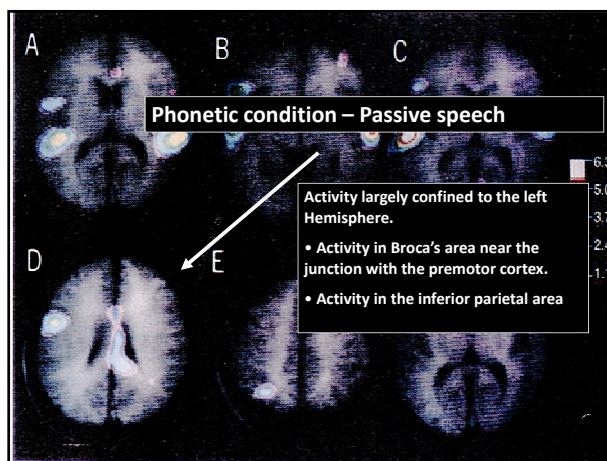
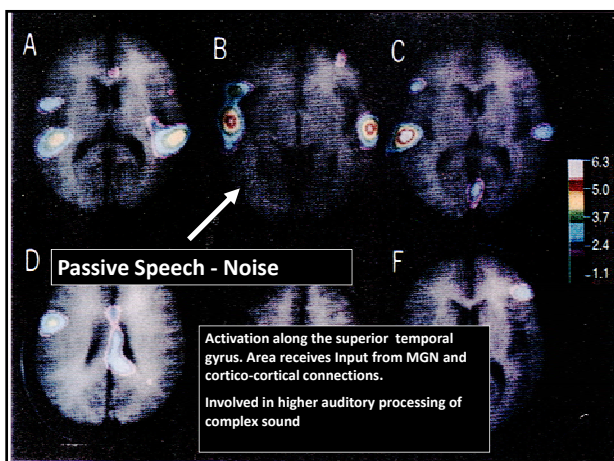
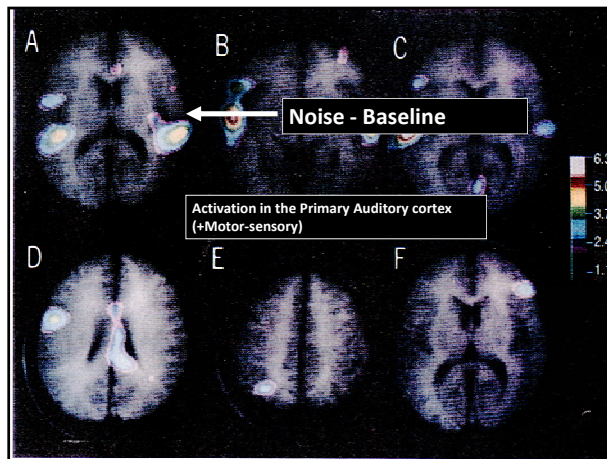
Two tasks:

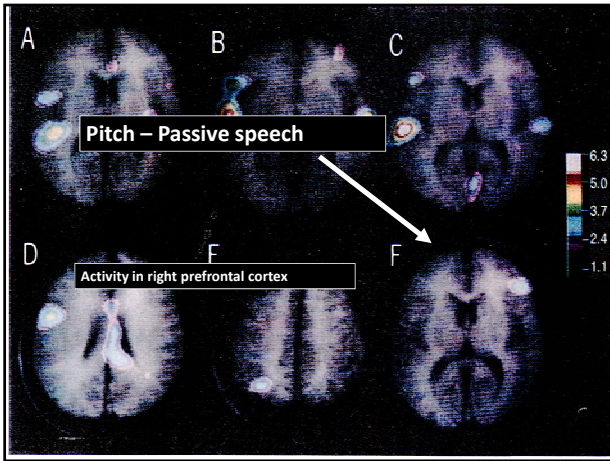
- Categorization of pitch direction (rising/falling)
- Categorization of duration (short/long)

Brechman & Scheich, 2005

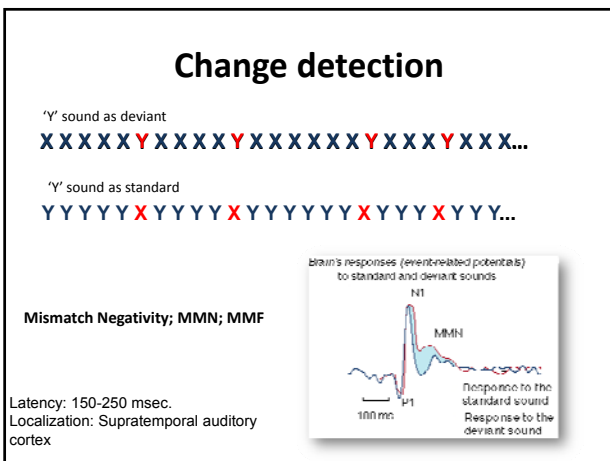
• Zatorre et al (1992) “Lateralization of Phonetic and Pitch Discrimination in Speech Processing”

Condition	Stimulus	Required response
Baseline	Silence	
Noise	Noise bursts	Alternating key press
Passive speech	Speech syllables	Alternating key press
Phonetic	Speech syllables	Key press to same final consonant
Pitch	Speech syllables	Key press to rising pitch





- ### Outline:
- Introduction to brain imaging techniques.
 - Spatial processing
 - Pitch and melody
 - Attention
 - **Change detection and MMN**
 - Speech
 - Brain asymmetry



MMN as a tool:

- Which features of sound is cortex sensitive to?

©
 Risto Näätänen
 1978

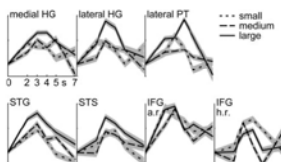
Brain mechanisms involved in the detection of acoustic changes

EEG + fMRI stimuli:

Sequences of click-trains of different lengths

- 100 ms (standard) ●
- 74 ms ●
- 52 ms ●
- 30 ms ●

Example trial:



Hemodynamic response time course in auditory cortex but not Frontal cortex is modulated by deviant size.

Schonwiesner et al, 2007

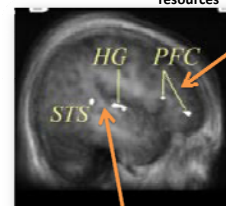
Brain mechanisms involved in the detection of acoustic changes

EEG + fMRI stimuli:

Sequences of click-trains of different lengths

- 100 ms (standard) ●
- 74 ms ●
- 52 ms ●
- 30 ms ●

Example trial:



Initial detection of change

Schonwiesner et al, 2007

Attention

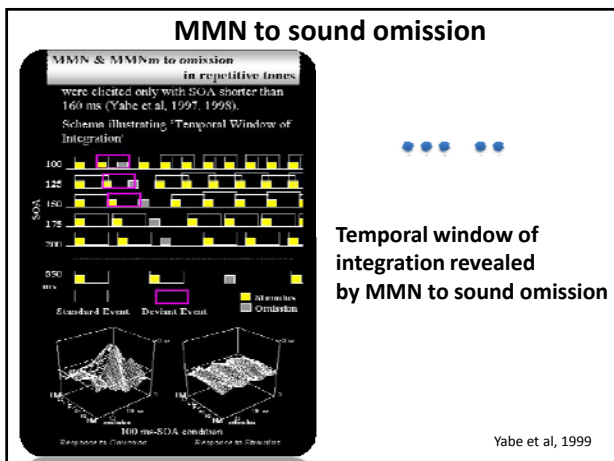
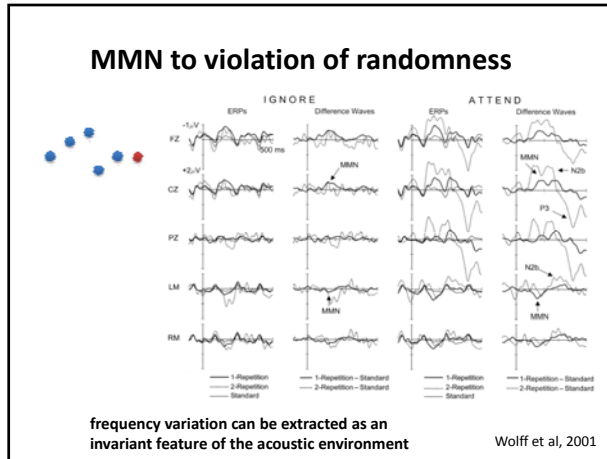
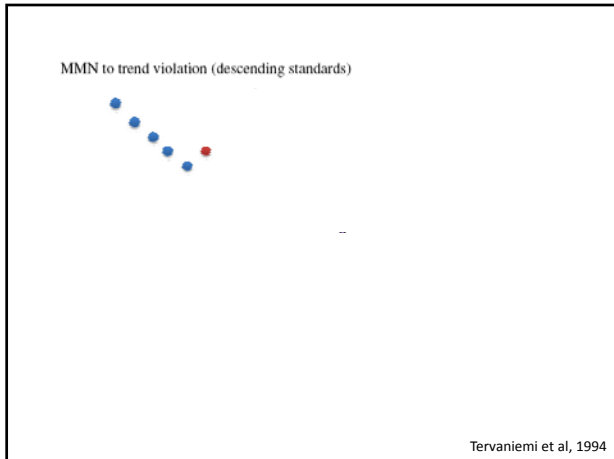


MMN as a tool:

- Which features of sound is cortex sensitive to?
- relationship to attention
- Allows to tap internal scene organization



© Risto Näätänen 1978



- Outline:
- Introduction to brain imaging techniques.
 - Spatial processing
 - Pitch and melody
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 - Change detection and MMN
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 - Brain asymmetry

Noise - silence Passive speech - noise

Phonetic judgement – passive speech Pitch judgement – passive speech

- signal undergoes discrete processing stages in separate neural subsystems
- A1 = early acoustic analysis of all signals
secondary areas = higher order processing
- When making a phonetic judgment subjects access an **articulatory representation** involving neural circuits that include Broca's area.

Zatorre et al, 1994

Language specific phoneme representations revealed by MMN

Naatanen et al, 1997

Language specific phoneme representations revealed by MMN

EEG stimuli:
MMN design

- /e/ (standard)
- /ø/
- /o/
- /æ/ non phoneme in either language
- /ð/ non phoneme in Finnish only

Naatanen et al, 1997

Language specific phoneme representations revealed by MMN

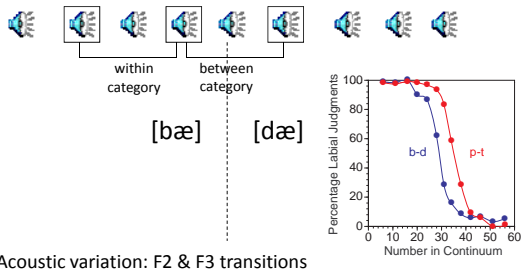
EEG stimuli:
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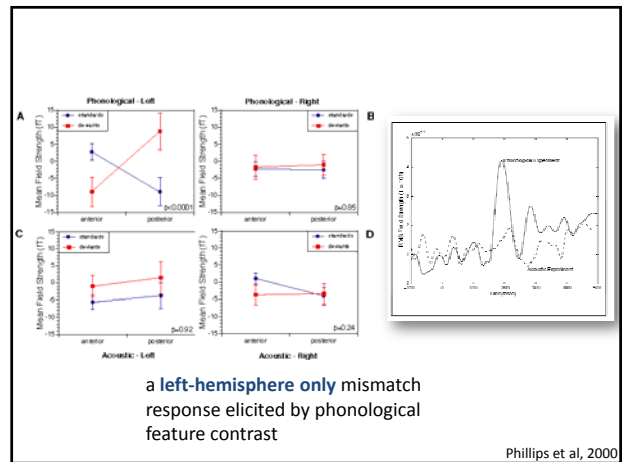
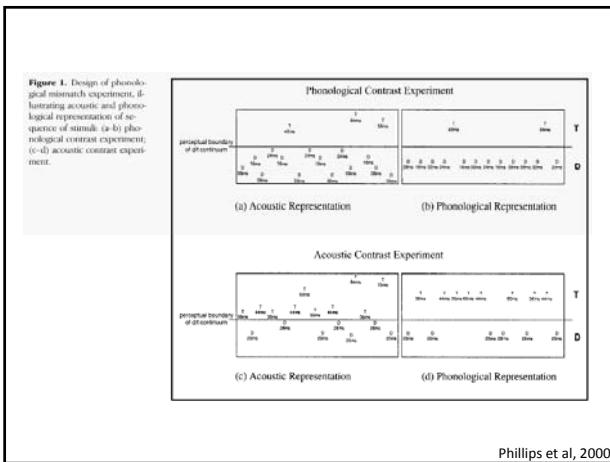
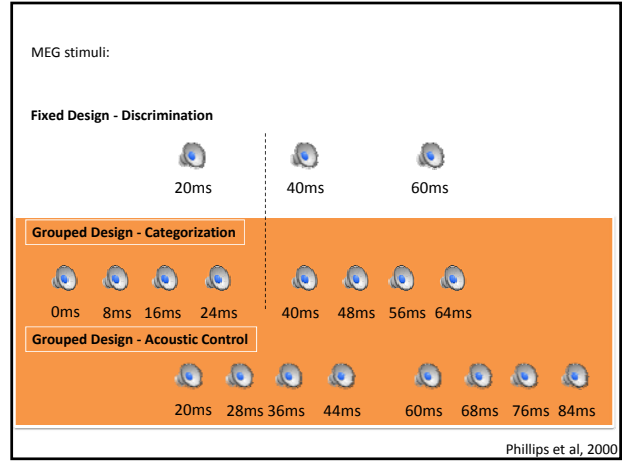
The native language of a listener affects auditory cortical responses to speech sounds

Naatanen et al, 1997

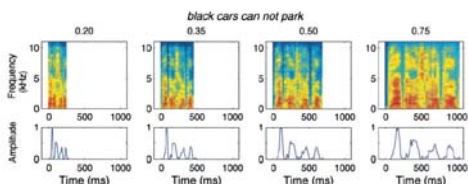
Phonetic categories in auditory cortex



- Acoustic variation: F2 & F3 transitions



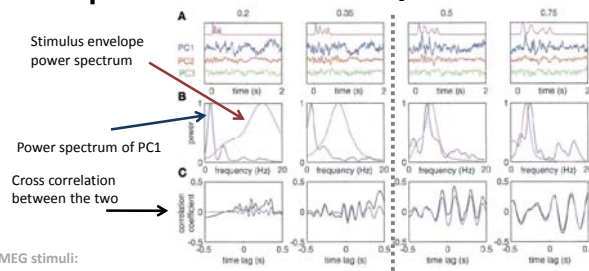
Speech comprehension and response patterns from auditory cortex



MEG stimuli:
 Time compressed sentences
 •0.75 least compressed
 •0.5
 •0.35
 •0.2 most compressed

Ahissar et al, 2001

Speech comprehension and response patterns from auditory cortex



MEG stimuli:
 Time compressed sentences
 •0.75 least compressed
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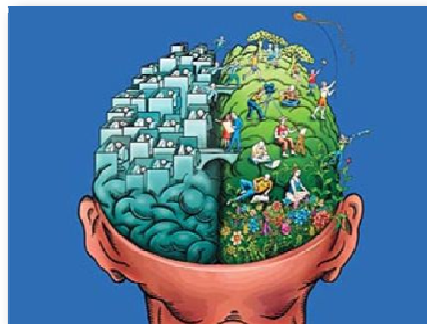
Bad intelligibility | Good intelligibility

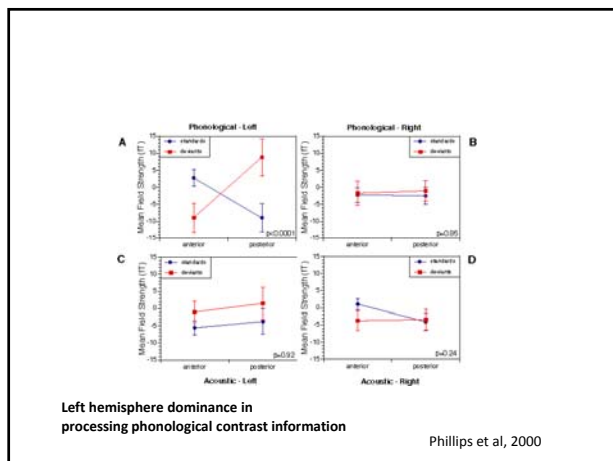
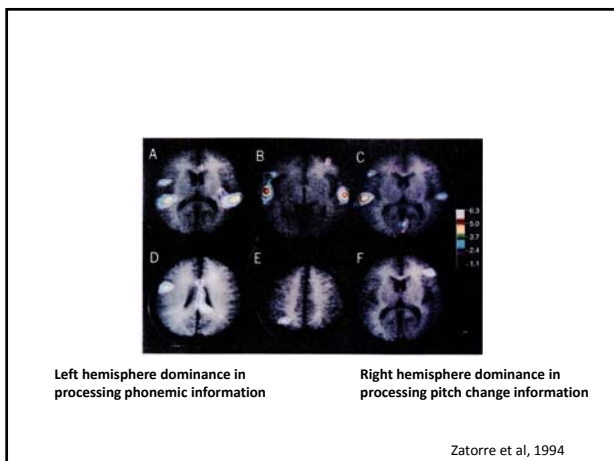
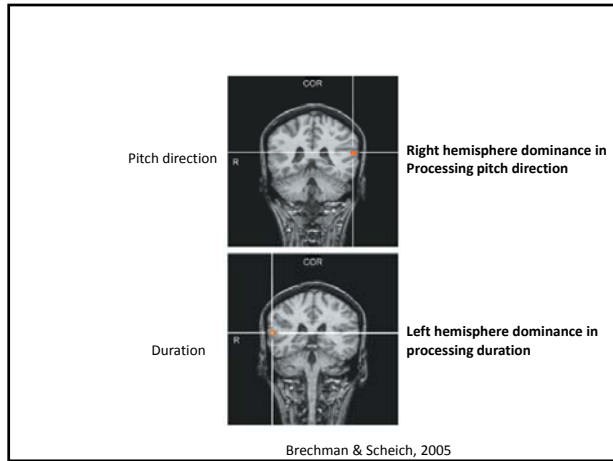
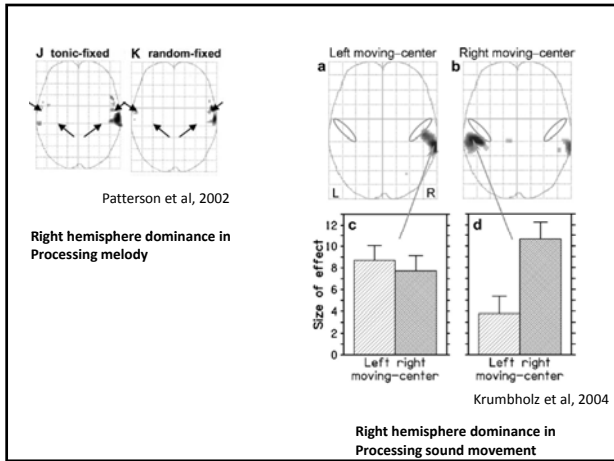
Intelligibility is correlated with the ability of auditory cortex to follow the temporal modulations of the signal

Ahissar et al, 2001

Outline:

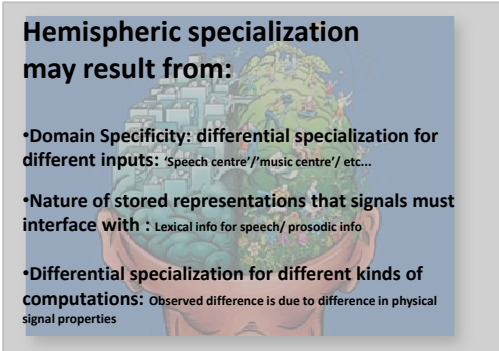
- Introduction to brain imaging techniques.
- Spatial processing
- Pitch and melody
- Attention
- Change detection and MMN
- Speech
- Brain asymmetry





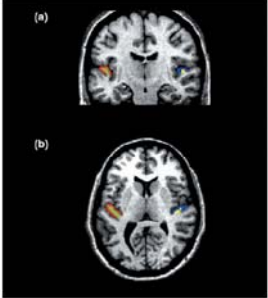
Hemispheric specialization may result from:

- **Domain Specificity:** differential specialization for different inputs: 'Speech centre'/'music centre' / etc...
- **Nature of stored representations that signals must interface with:** Lexical info for speech/ prosodic info
- **Differential specialization for different kinds of computations:** Observed difference is due to difference in physical signal properties



Anatomical asymmetries in human auditory cortex

Greater volume of HG in the Left Hemisphere



TRENDS in Cognitive Sciences

from Zatorre et al, 2002

Spectral and temporal processing in human auditory cortex

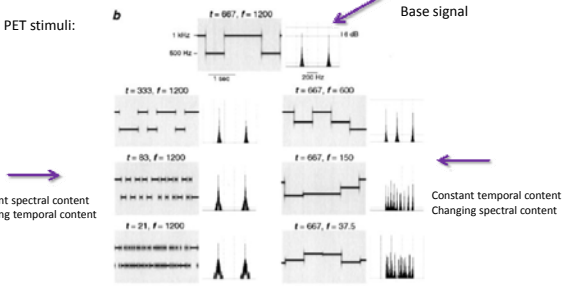
- **Hypothesis #1:**
Human auditory cortex is functionally segregated such that differences exist in the temporal and spectral resolving power between the two hemispheres

Speech requires good temporal resolution
Music requires good spectral resolution

Zatorre & Belin, 2001

Spectral and temporal processing in human auditory cortex

PET stimuli:



Zatorre & Belin, 2001

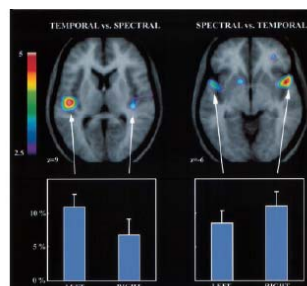
Spectral and temporal processing in human auditory cortex



■ Covariation of activation with rate of **spectral** change
■ Covariation of activation with rate of **temporal** change

Zatorre & Belin, 2001

Spectral and temporal processing in human auditory cortex



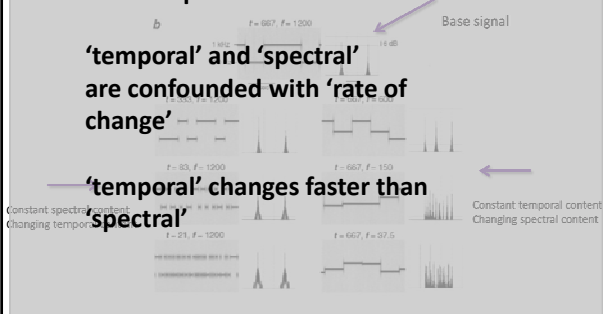
Zatorre & Belin, 2001

Spectral and temporal processing in human auditory cortex

Possible problem:

'temporal' and 'spectral' are confounded with 'rate of change'

'temporal' changes faster than 'spectral'



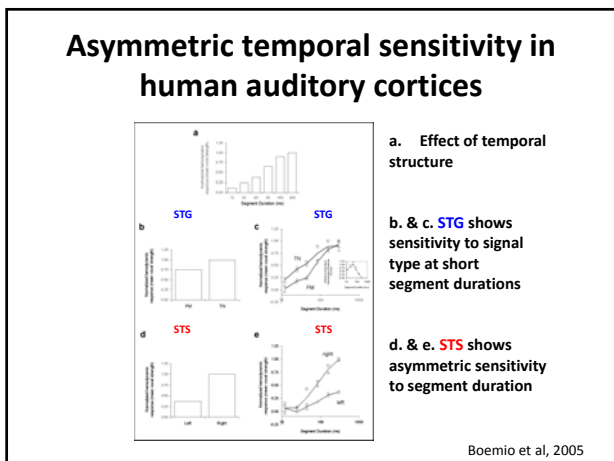
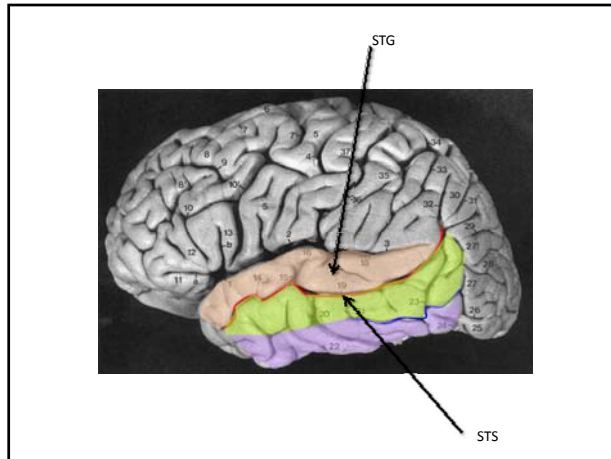
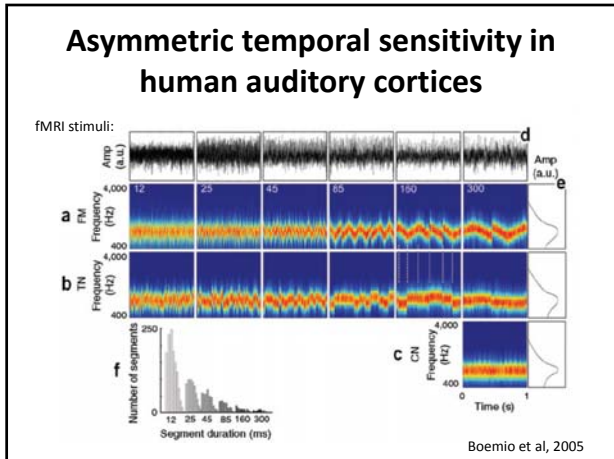
Zatorre & Belin, 2001

Asymmetric temporal sensitivity in human auditory cortices

- Hypothesis #2:**
 Human auditory cortex is functionally segregated such that differences exist in the temporal resolving power between the two hemispheres

Two time scales: 'fast' (25-50 ms)
'slow' (200-300 ms)

Boemio et al, 2005



Hemispheric specialization may result from:

- **Domain Specificity:** differential specialization for different inputs: 'Speech centre'/'music centre' / etc...
- **Nature of stored representations** that signals must interface with : Lexical info for speech/ prosodic info
- **Differential specialization for different kinds of computations:** Observed difference is due to difference in physical signal properties

Brain Asymmetry summary

+ homage to David Poeppel

