Harvard-MIT Division of Health Sciences and Technology
HST.722J: Brain Mechanisms for Hearing and Speech
Course Instructor: Jennifer R. Melcher

HST 722
Brain Mechanisms for Hearing and Speech

October 27, 2005
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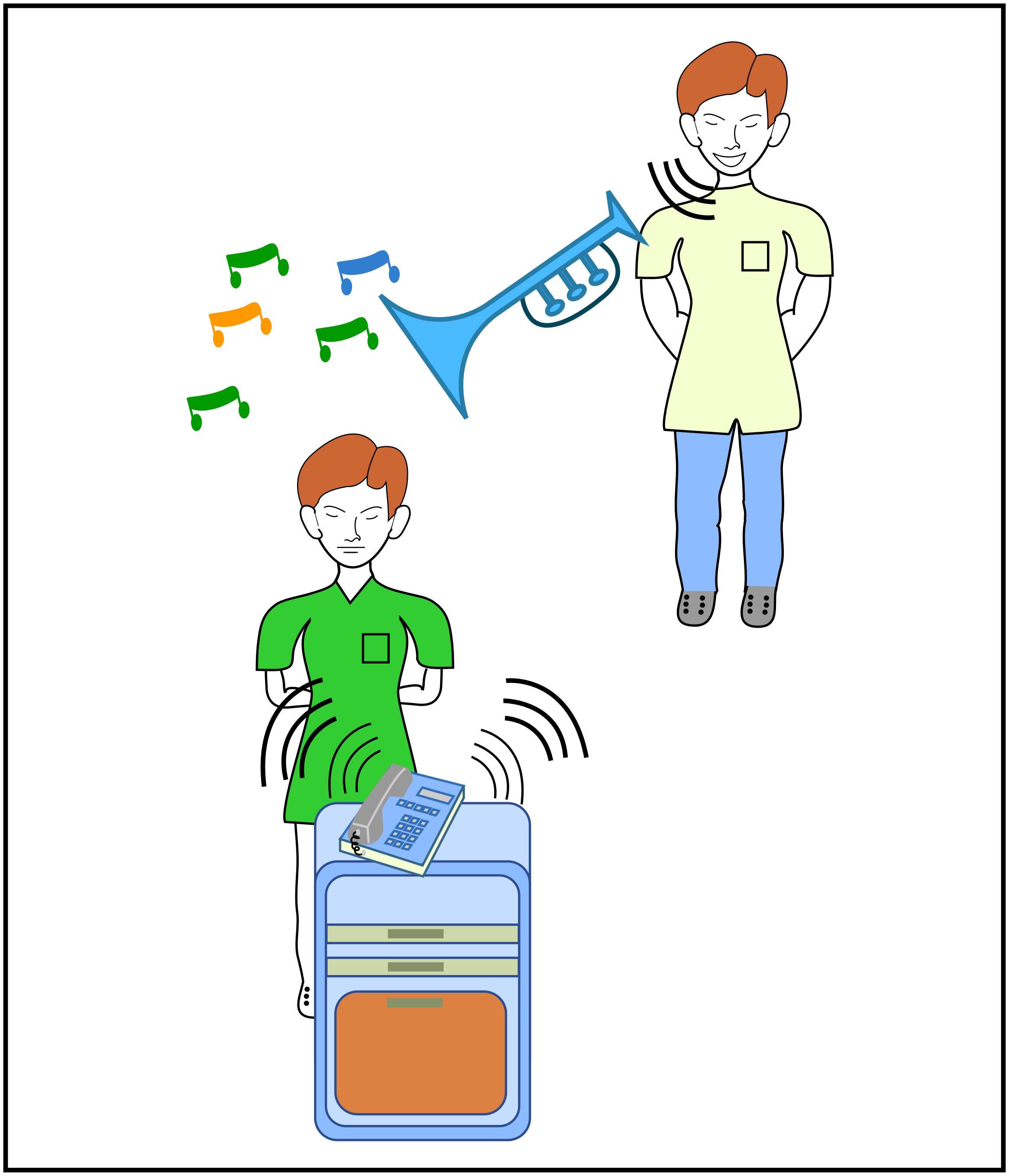
Neuroimaging Correlates of Human Auditory Behavior

"The Problem"



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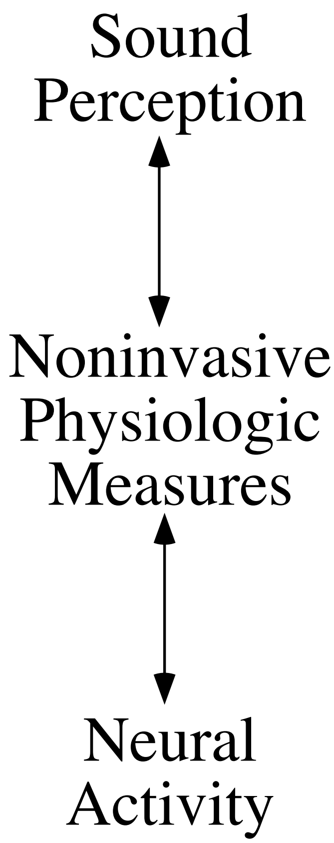

Sound Perception
Noninvasive Physiologic Measures
Neural Activity

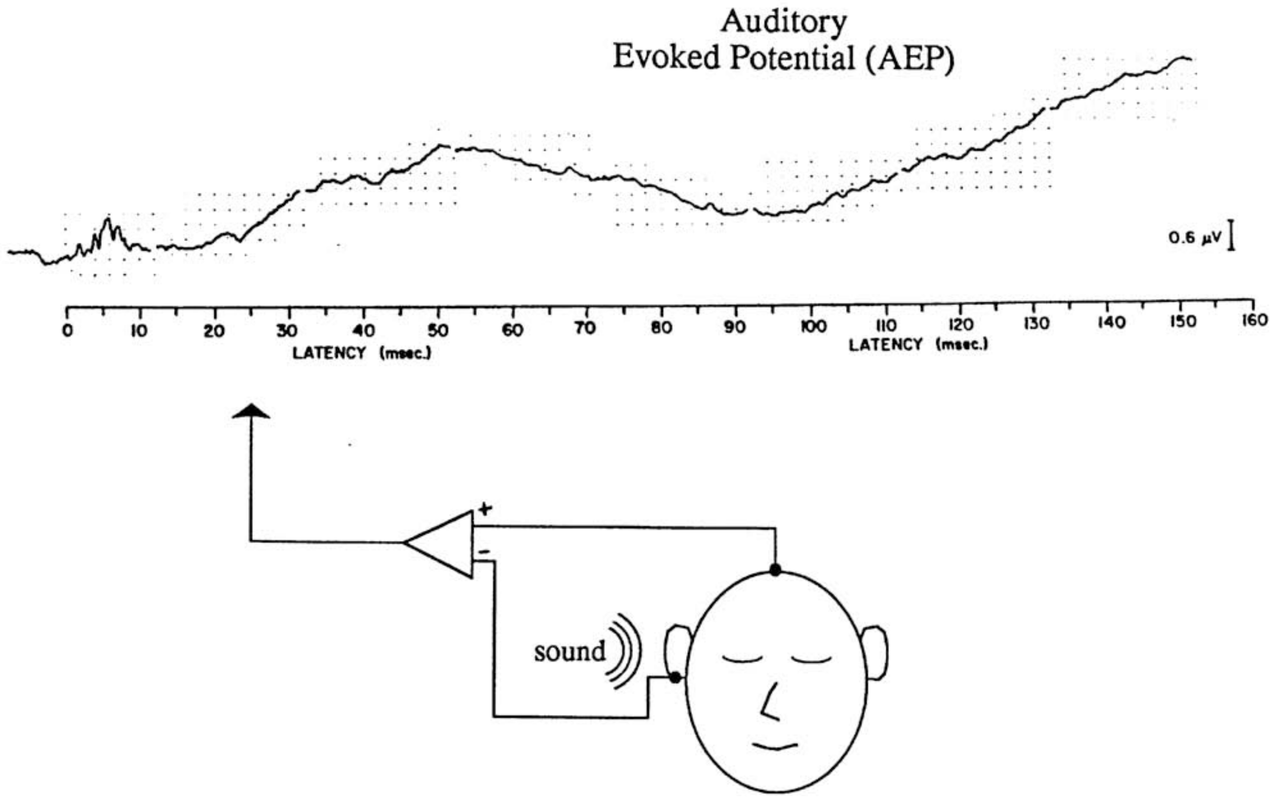
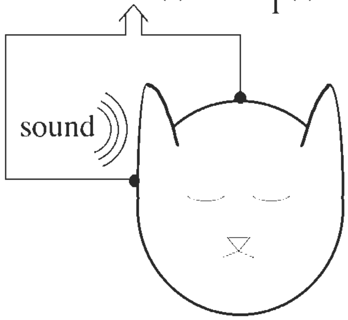


Figure above illustrates how auditory evoked potentials are measured. Potential shown was evoked by a click stimulus and was recorded in a human subject. Waveform is the averaged response to many click presentations. (AEP record from R.A. Levine)
(Courtesy of Robert Aaron Levine. Used with permission.)

General Picture of Auditory Evoked Potential Generation

(1) $$AEP(t) = V_1(t) + V_2(t) + \ldots + V_k(t) + \ldots$$



$V_k(t)$: potential produced by the kth cell population

(2) $$V(t) = \sum_{i=1}^{N} v_i(t)$$

N: number of cells in the population

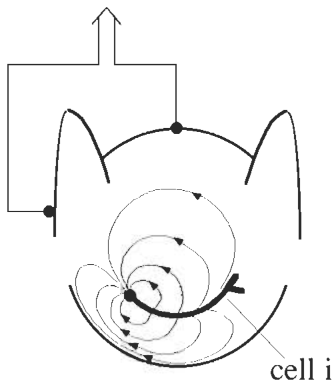
$V(t)$: potential produced by a particular population

$v_i(t)$: potential produced by one cell in that population

(3) $$v_i(t) = u_i(t) * r_i(t)$$

$u_i(t)$ = unitary potential (potential produced each time cell i discharges)

$r_i(t)$ = instantaneous discharge rate (instantaneous rate at which cell i discharges following the AEP stimulus)



(4) $$V(t) = \sum_{i=1}^{N} u_i(t) * r_i(t) = u(t) * \sum_{i=1}^{N} r_i(t) = u(t) * R(t)$$

$R(t)$: compound instantaneous discharge rate

(5) Factors affecting the amplitude of V(t):

- number of cells in the population
- degree to which cells in the population discharge in synchrony with each other
- amplitude of u(t), r(t)

(see Goldstein and Kiang, 1958; Wang, 1979; Melcher and Kiang, 1996)

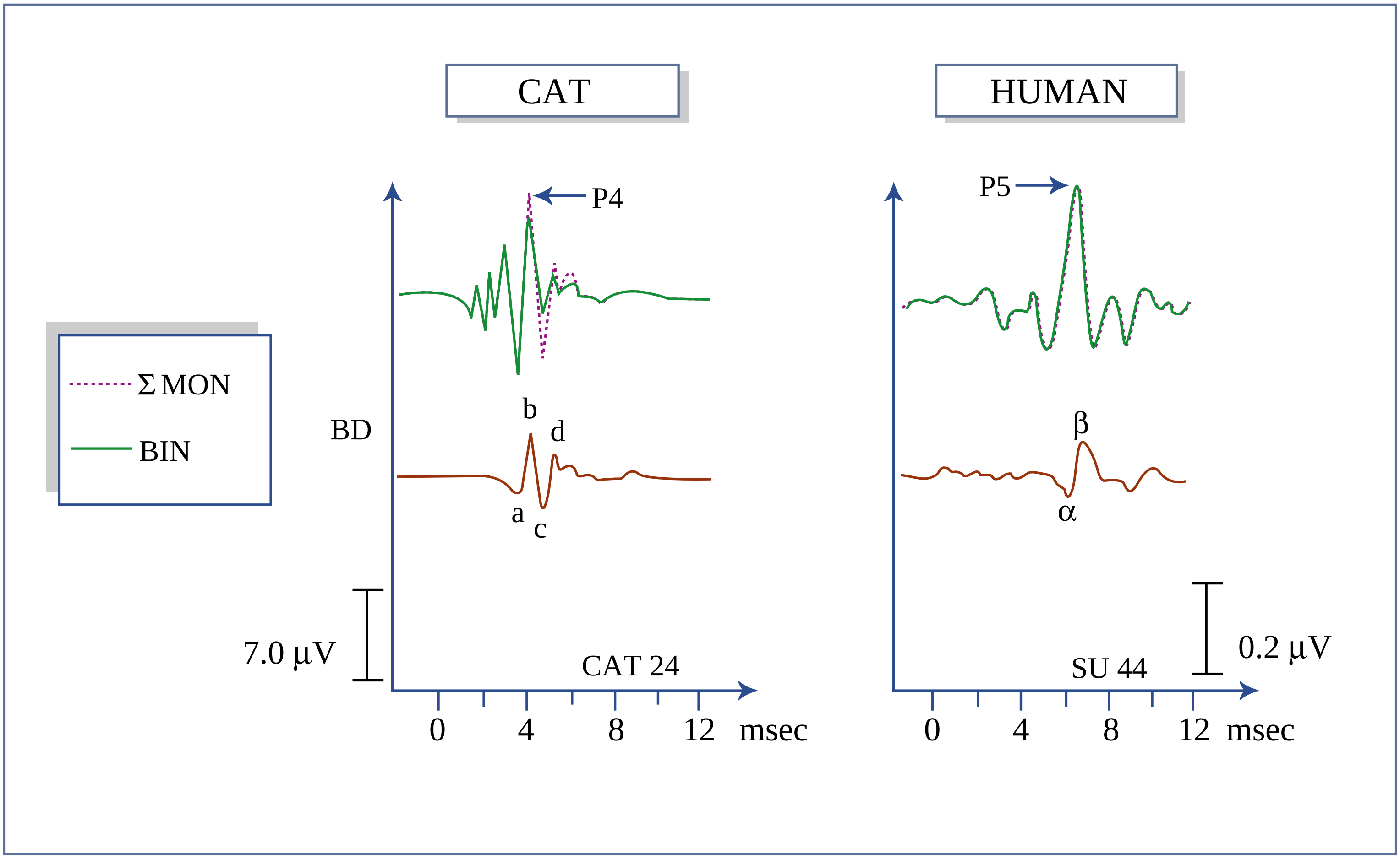
Furst et al. (1985) *“Click lateralization is related to the β component of the dichotic brainstem auditory evoked potentials of human subjects”*

For binaural clicks with different ITDs and ILDs, quantified

- perception
- binaural difference potential

- Attributes of the binaural difference are correlated with the perception of binaural sound.

Binaural Difference Potential

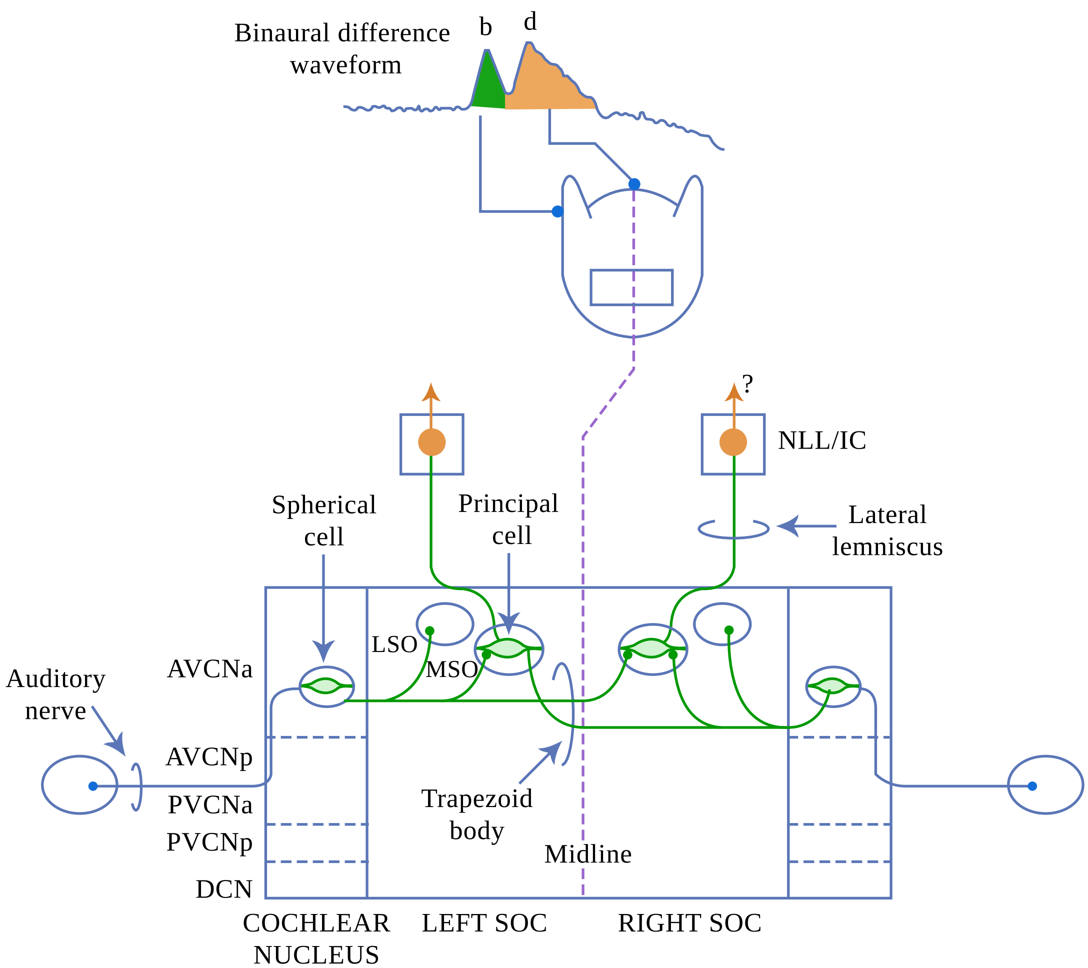


Figures by MIT OCW.

Fig. 9. Binaural, sum of the monaurals, and binaural difference waveforms for both species. The binaural (solid lines) and sum of the monaural waveforms (dotted lines) are superimposed. The difference between these two waveforms, the binaural difference (BD) waveform, is plotted below. The recording electrodes were vertex to nape for both species. Stimuli were 10/sec; rarefaction clicks at 40 dB SL for the cat and 38 dB HL for the human. (from Fullerton et al., 1987)

- Binaural difference (BD) is derived from BAEPs evoked by monaural and binaural stimuli (above). BAEP: brainstem auditory evoked potential
- The BD reflects an interaction between converging signals from the two ears at the level of the brainstem.

Cellular Generators of the Binaural Difference Potential



Cellular generators of the binaural difference potential in cat. Green color indicate the generators of the first peak ('b'; white on black) and possible generators of the second peak ('d'; black on white). The schematic of the lower auditory system (at bottom) shows the generators' relationship to other cells. NLL, nuclei of the lateral lemniscus; IC, inferior colliculus.

Figure by MIT OCW.

Cellular generators of the binaural difference potential in cat. Diagonal line shadings indicate the generators of the first peak (‘b’; white on black) and possible generators of the second peak (‘d’; black on white). The schematic of the lower auditory system (at bottom) shows the generators’ relationship to other cells. NLL, nuclei of the lateral lemniscus; IC, inferior colliculus.

(From Melcher, 1996)

Discussion Questions:

- If the generator results are combined with the findings of Furst et al., what can be said about the neural processing underlying sound lateralization and binaural fusion?
- We generally think of the MSO as a coincidence detector. Are Furst et al.'s binaural difference data consistent with this idea?

Late Responses: dependence on attention and stimulus context

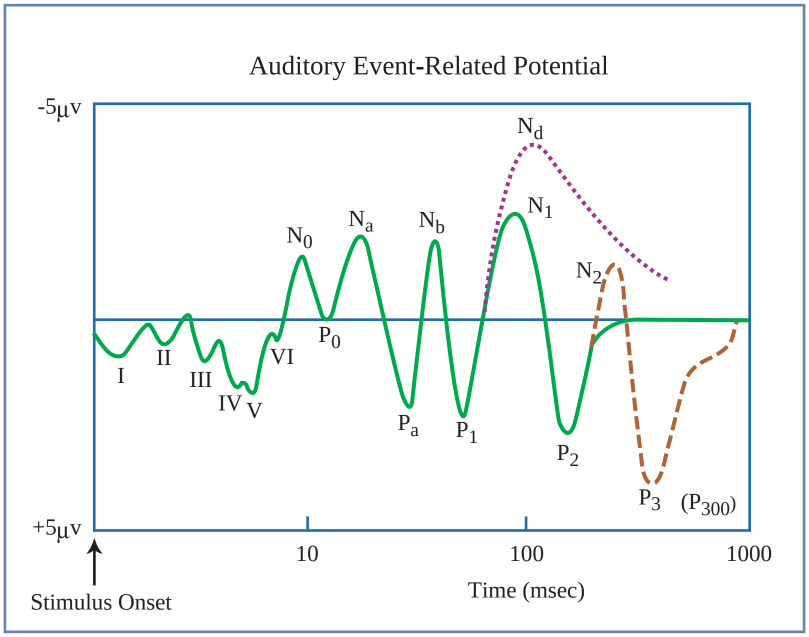


Figure by MIT OCW.

Idealized AEP evoked by transient stimuli (___) including components that are dependent on stimulus context and subject attention (….. , -----). (from Hillyard and Kutas, 1983; also see Hillyard et al., 1973; Donchin et al., 1978).

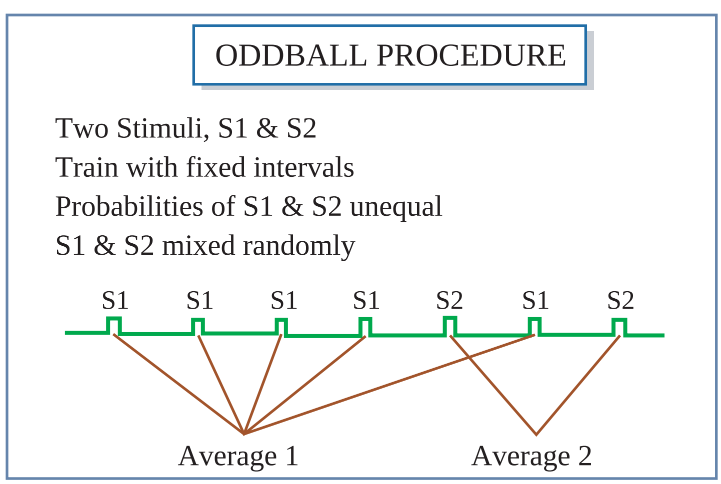
Nd - or "processing negativity"
- produced when the subject attends to the stimuli
- visualized by taking the difference between responses to attended and unattended stimuli

N2 - or "N2000", "mismatch negativity
- occurs in response to "rare" stimuli (S2 below) in oddball paradigm
- can occur even when the subject is not attending to the stimuli
- dependent on stimulus modality (e.g. auditory vs. visual)

P3 - or "P300"
- occurs in response to "rare" stimuli (S2 below) in oddball paradigm when the subject is attending to the stimuli
- independent of stimulus modality

Figure 1-12. Schematic diagram of oddball stimulus presentation paradigm for P300 measurement (from Squires & Hecox, 1983). Selected measurement parameters are indicated. Responses are averaged separately for Stimulus Type 1 (i.e. the frequent stimulus) and Stimulus Type 2 (i.e. the rare or oddball stimulus). *Note*. From "Electrophysiological Evaluation of Higher Level Auditory Processing" by K.C. Squires and K.E. Hecox, 1983, *Seminars in Hearing, 4 (4),* p. 422. Reprinted by permission.

(from Hall, 1992)



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N2 (N200), P3 (P300)

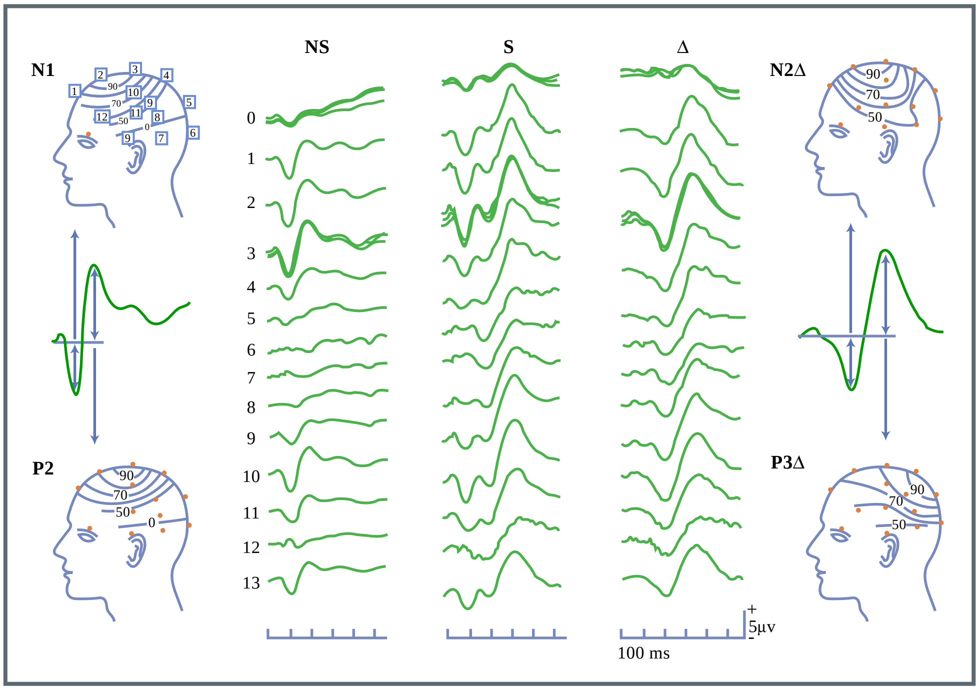


Figure by MIT OCW.

Fig. 1. Mean for eight subjects of the non-signal (NS), signal (S) and difference (Δ) waveforms at each electrode site in the auditory condition. Isopotential topographic distributions are expressed as percentages of maximum response amplitude for the N1 and P2 components of the non-signal response (left) and the negative (N2 Δ) and positive (P3 Δ) components of the Δ waveform (right). Supraorbital (0) and vertex (electrode 3) traces from the 3 runs are superimposed.

(From Simson et al., 1977)

NS - responses to standard stimuli (2000 Hz tone bursts)

S - responses to rare stimuli (1000 Hz tone bursts)

Δ - response to rare stimuli minus response to standard stimuli

Fig. 4. Frontal, vertex, and parietal (across-subjects averaged) difference waveforms obtained by subtracting the ERP to the 1000-Hz standard stimulus from that to the 1044-Hz deviant stimulus at different deviant-stimulus probabilities. The continuous line indicates the counting condition and the broken line the ignore condition. The amplitude of the fronto-centrally distributed MMN is decreased when the probability is increased from 2% to 10%. When the two stimuli are equiprobable, no MMN is seen.

From Sams et al., 1985)

MMN - mismatch negativity

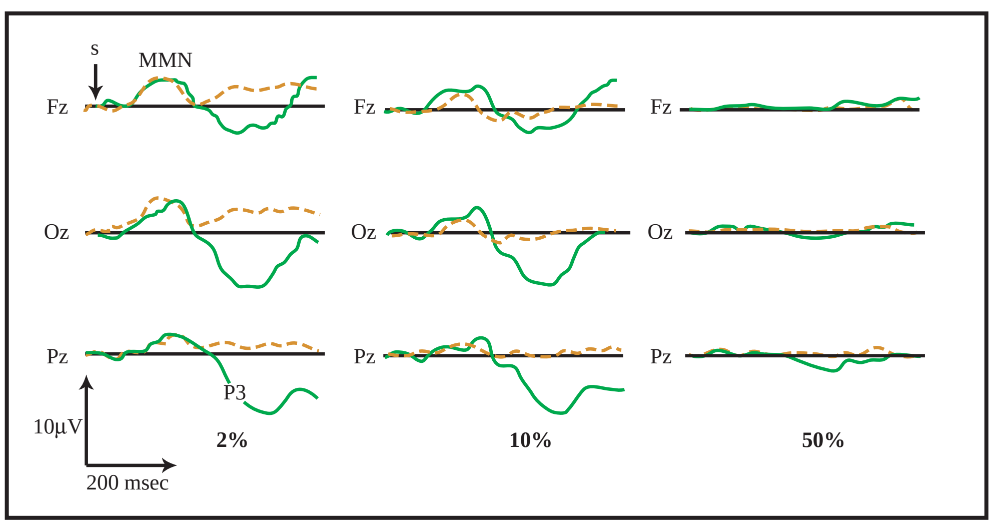


Figure by MIT OCW.

Kraus et al. (1996) *“Auditory neurophysiologic responses and discrimination deficits in children with learning problems”*

- Stimuli: Syllables, varied along two continua

- Subjects: Children with and without learning problems

- Measured discrimination and mismatch negativity

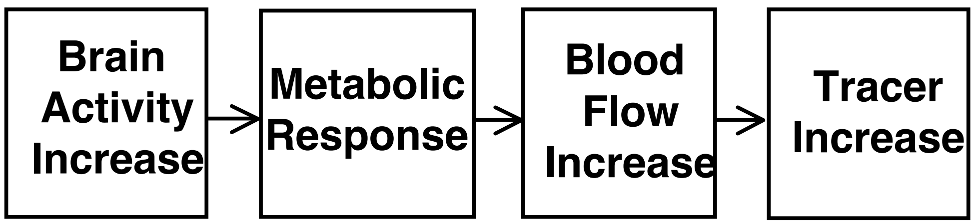
- The children with learning problems showed
  - deficits in their ability to discriminate syllables
  - abnormally small mismatch negativity

<u>Conclusion</u>

The behavioral deficits in the children with learning problems arose at a processing stage that precedes conscious perception.

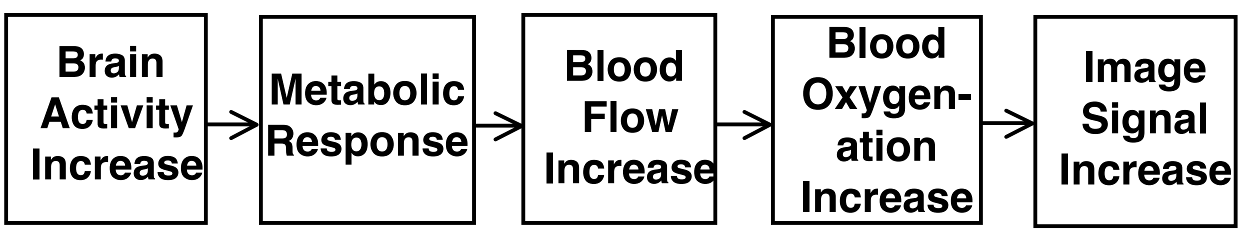
PET

(radioactive tracer e.g., radio-labeled H_2O)

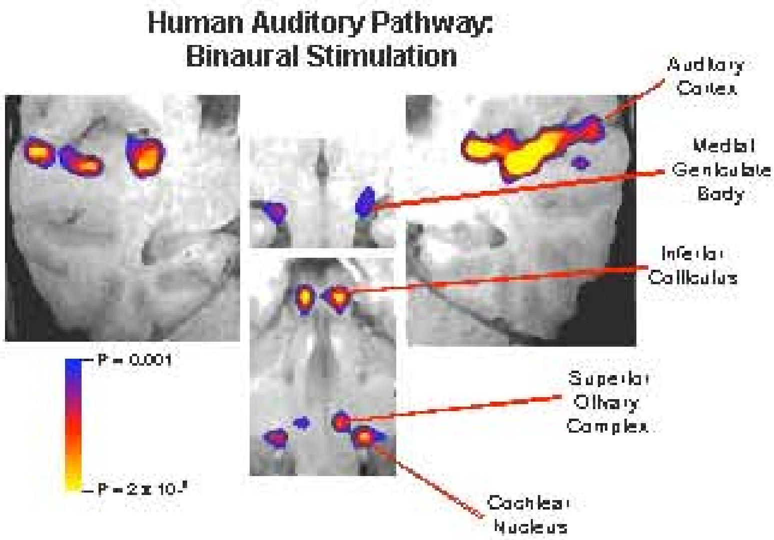


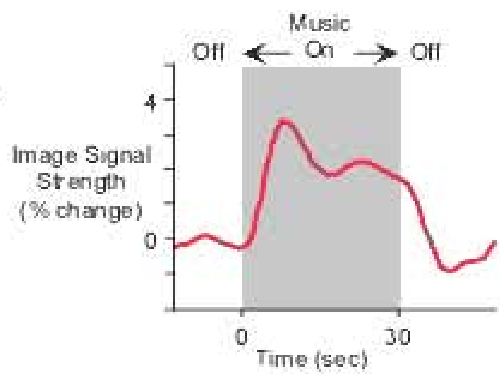
fMRI

(Blood Oxygenation Level-Dependent (BOLD))



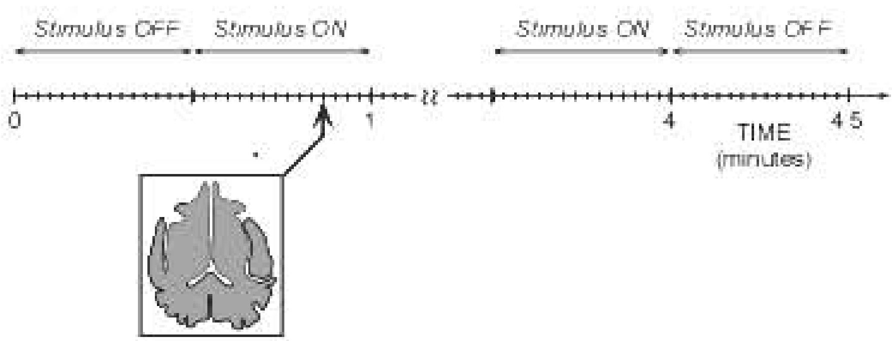
Functional Magnetic Resonance Imaging (fMRI)

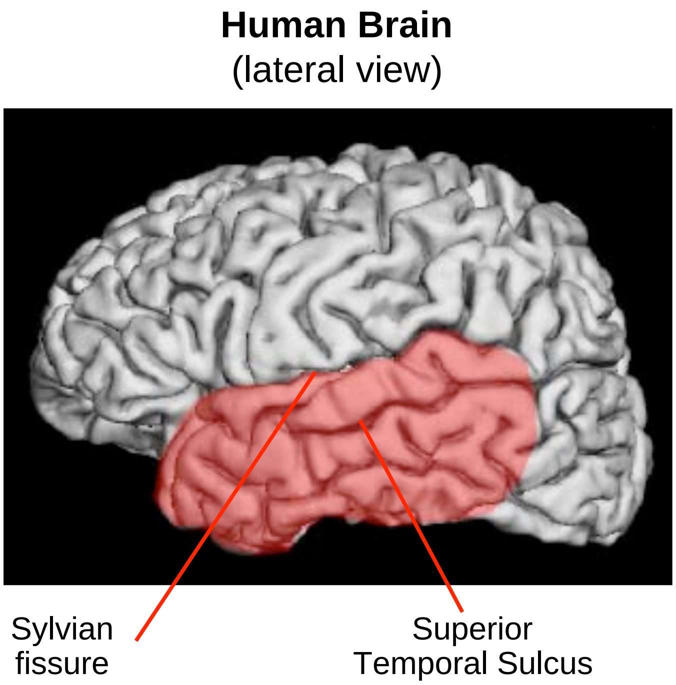


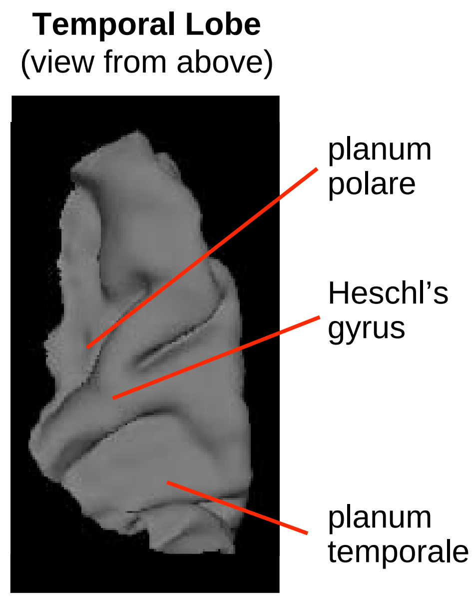


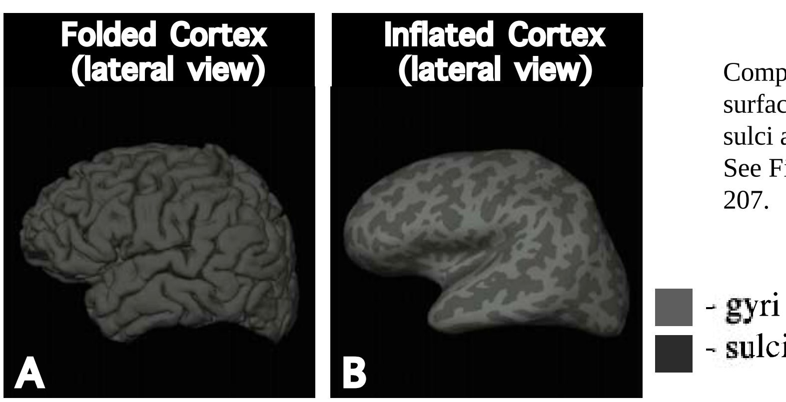
Above, left: fMRI activation in brainstem, thalamic and cortical auditory centers. Each panel shows a color activation map superimposed on an anatomical image intersecting one or more auditory structures. The presence of color indicates a statistically significant ($p < 0.001$) difference in image signal between stimulus "on" and "off" periods. Color indicates signficance level. The . Slice thickness: 5-7 mm. In-plane resolution for functional imaging: 3x3 mm.
Above, right: Image signal vs. time in auditory cortical areas showing activation.

Paradigm commonly used to obtain fMRI activation maps. Stimulus "on" periods are alternated with stimulus "off" periods while MR images are acquired at regular intervals. Tic marks on time axis indicate image acquisition times. A sample image is shown at one interval.









Computational inflation of the cortical surface. In the inflated format, the cortex of sulci and gyri can be viewed simultaneously. See Fischl et al. (1999) NeuroImage 9: 195-207.

Scott et al. (2000) *"Identification of a pathway for intelligible speech in the left temporal lobe"*

- Four stimulus conditions that included speech and several forms of degraded speech:
  - speech
  - noise-vocoded speech
  - rotated speech
  - rotated, noise-vocoded speech

- The stimuli differed in
  - intelligibility
  - presence of phonetic information
  - presence of pitch variations

- PET activity was compared between conditions.

<u>Conclusion</u>

Processing unique to intelligible speech is performed anteriorly in the left superior temporal sulcus, while lower-level processing is performed more posteriorly in the left STS and STG.

Discussion Questions:

- Scott et al. argue that their choice of stimuli may be better than previous ones for identifying sites of speech-specific processing. Do you agree?

- What assumptions have been made about the relationship between brain activity and the functional specificity of a brain region?

Beauchamp et al. (2004) *"Unraveling multisensory integration: patchy organization within human STS multisensory cortex"* Nat. Neurosci. 7: 1190-1192.

- Three stimulus conditions:
  - visual (videos of tools or faces)
  - auditory (sounds of tools or voices)
  - audio-visual (simultaneous images and sounds)

- High resolution fMRI of the superior temporal sulcus, a known region of multimodal convergence

- Three types of cortical patches were identified having:
  - auditory > visual response
  - visual > auditory response
  - auditory = visual

<u>Conclusion</u>

"A model… suggested by our data is that auditory and visual inputs arrive in the STS-MS in separate patches, followed by integration in the intervening cortex."

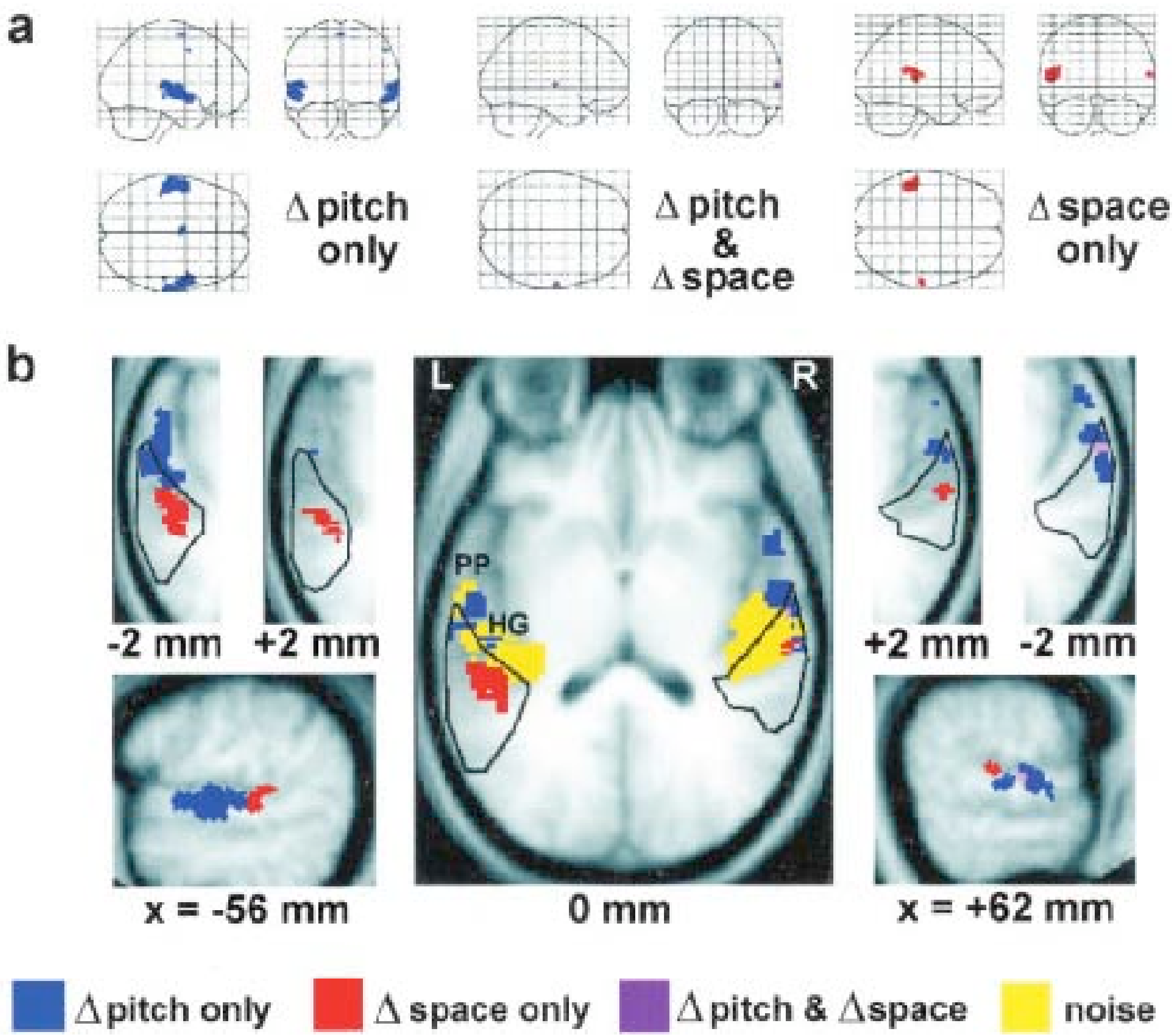


Figure 2. Statistical parametric maps for contrasts of interest (group data). a, SPMs are shown as "glass brain" projections in sagittal, coronal, and axial planes. b, SPMs have been rendered on the group mean structural MRI brain image, normalized to the MNI standard stereotactic space (Evans et al., 1993). Tilted axial sections are shown at three levels parallel to the superior temporal plane: 0 mm (center), +2 mm, and -2 mm (insets). The 95% probability boundaries for left and right human PT are outlined (black) (Westbury et al., 1999). Sagittal sections of the left (x = -56 mm) and right (x = +62 mm) cerebral hemispheres are displayed below. All voxels shown are significant at the $p < 0.05$ level after false discovery rate correction for multiple comparisons; clusters less than eight voxels in size have been excluded. Broadband noise (without pitch) compared with silence activates extensive bilateral superior temporal areas including medial Heschl's gyrus (HG) (b, center, yellow). In the contrasts between conditions with changing pitch and fixed pitch and between conditions with changing spatial location and fixed location, a masking procedure has been used to identify voxels activated only by pitch change (blue), only by spatial change (red), and by both types of change (magenta). The contrasts of interest activate distinct anatomical regions on the superior temporal plane. Pitch change (but not spatial location change) activates lateral HG, anterior PT, and planum polare (PP) anterior to HG, extending into superior temporal gyrus, whereas spatial change (but not pitch change) produces more restricted bilateral activation involving posterior PT. Within PT (b, axial sections), activation attributable to pitch change occurs anterolaterally whereas activation attributable to spatial change occurs posteromedially. Only a small number of voxels within PT are activated both by pitch change and by spatial change.

Figures 2a, 2b from Warren, and Griffiths. "Distinct mechanisms for processing spatial sequences and pitch sequences in the human auditory brain." *J Neurosci* 23 (2003): 5799-5804.

Zimmer and Macaluso (2005) *“High binaural coherence determines successful sound localization and increased activity in posterior auditory areas”*

- Main Experiment:
  - fMRI and behavioral measurements during sound localization
  - manipulate sound location using ITD
  - manipulate ability to localize by manipulating binaural coherence
  - identify brain areas showing a correlation between activation and localization performance

- Control Experiments:
  - separated activation specifically correlated with localization performance from activation correlated with binaural coherence.

<u>Conclusion</u>

Within the superior temporal plane, only planum temporale showed activation specifically correlated with localization performance. It was concluded that binaural coherence cues are used by this region to successfully localize sound.

Do sound recognition and sound localization involve segregated networks (i.e., "what" and "where" pathways)? This question was addressed by Maeder and coworkers (2001). In an fMRI experiment, subjects were imaged in three conditions: (1) during a localization task, (2) during a recognition task, and (3) at rest (see right).

FIG. 1 Schematic representation of the experimental paradigm, the blocks and the temporal structure of the stimuli. L = localization task; R = recognition task; r = rest.

Ventral cortical areas showed greater activity during the recognition task (green, below), while dorsal areas showed greater activity during localization (red, below).

FIG.5 Active paradigm: 3-D projections of activation on smoothed normalized brain (group results). Areas more activated in recognition than localization are shown in green, areas more activated in localization than in recognition are shown in red.
Adapted from Maeder et al. (2001) NeuroImage 14: 802-816.

Lewald et al. (2002) *"Role of the posterior parietal cortex in spatial hearing"* J. Neurosci. 22: RC207.

- Subjects performed a sound lateralization task before and after cortical stimulation using transcranial magnetic stimulation (TMS)

- TMS: a noninvasive stimulation method that reversibly alters neuronal function

- Stimuli: Dichotic tones with various ITDs

- Task: indicate perceived location (left or right)

- Stimulation site: posterior parietal lobe

<u>Conclusion</u>

TMS produced a shift in sound lateralization, suggesting a role for posterior parietal cortex in spatial hearing.

“What” and “Where” Pathways of the Visual System

Figure removed due to copyright reasons.
Please see:

Posner, M. I., and M. E. Raichle. *Images of the Mind*. New York, NY: Scientific American Library, 1994.

The “what” and “where” pathways in the visual system include areas specialized for processing depth perception (symbolized by a pair of spectacles), form (an angle), color, and direction (the curve ahead sign). The result is object recognition (the “what” pathway) or object location (the “where” pathway).

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fMRI: Mitigation of Scanner Acoustic Noise

Clustered Volume Acquisition: A method for removing the impact of scanner acoustic noise on auditory fMRI activation

Figure removed due to copyright reasons.
Please see:
Edmister, et al. *Human Brain Mapping* 7 (1999): 89-97.

Slide 7:
Fullerton, B. C., R. A. Levine, H. L. Hosford-Dunn, and N. Y. Kiang. "Comparison of cat and human brain-stem auditory evoked potentials." *Electroencephalogr Clin Neurophysiol* 66, no. 6 (Jun 1987): 547-70.

Slide 8:
Melcher, J. R. "Cellular generators of the binaural difference potential." *Hear Res* 95 (1996): 144-160.

Slide 10 (Top figure):
Hillyard, S. A. and M. Kutas. "Electrophysiology of cognitive processing." *Ann Rev Psychol* 34 (1983): 33-61.

Slide 10 (Bottom figure):
Hall, James W. "Handbook of Auditory Evoked Re sponses." *Allyn and Bacon.* Boston, I, II, 1992.

Slide 11 (Top figure):
Simson, R., H. G. Vaughan, Jr., and W. Ritter. "The scalp topography of potentials in auditory and visual discrimination tasks." *Electroenceph clin Neurophysiol* 42 (1977): 528-535.

Slide 11 (Bottom figure):
Sams, M., K. Alho, and R. Näätänen. "The mismatch negativity and information processing." *Psychophysiological Approaches to Human Information Processing*. 1985.