Lateral Asymmetry in the Human Auditory System

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Outline

• Auditory Cortex is asymmetric and function is lateralized
• Auditory function may also be lateralized based on the ear of presentation: Physiologic measures—Psychophysical measures
• What is the extent of functional differences in the left and right ears
• What are the developmental trends in lateralized function
• What is the consequence of unilateral deafness?
Auditory Areas of the Left and Right Hemisphere are Physically and Functionally Asymmetrical

Typical MRI results on normal right-handed subject:
Greater white matter volume is found in left hemisphere Heschl’s gyrus. Zatorre 2001

Asymmetry of the auditory cortex (L>R) is present at birth.
Speech Primarily Activates Left Auditory Areas and Music activates the Right

PET Scans during Detection Task of CV or Musical Instruments
Hugdahl et al., 1999
PET scans show greater metabolic activity in right auditory areas in response to musical chords. And greater activity in the left hemisphere from phoneme stimulation.

Tervaniemi et al., 2000
Asymmetrical function of cerebral cortices

Damage studies (stroke, trauma & hemispherectomy) have shown that left hemisphere damage impairs speech perception while right hemisphere disorders impair music/tonal perception.

Sidiatis & Volpe, 1988
Johnsrude et al., 2000
Liegeois-Chauvel et al., 1998
Warrier & Zatorre, 2004
There is a significant body of literature demonstrating that the acoustic/temporal nature of the stimulus rather than the linguistic or musical nature that dictates the laterality of processing.

Rapidly changing, broadband or temporally complex stimuli are preferentially processed in the Left Hemisphere Primary Auditory areas and slowly changing or narrow band stimuli are more readily processed in the Right Hemisphere.

See Zatorre & Gandour, 2008 Phil Trans.R. Soc. B 363, 1087-1104.
Temporal and Spectral Aspects of *Non-Linguistic Stimuli* Dictates Laterality of Processing

Tonal sequences varied by rate of change (temporal) or frequency change (spectral). PET Scans show greater activation of left auditory areas for temporal changes and right hemisphere activation for spectral changes.

Zatorre & Belin 2001
Linguistic distinctions based on tonality are processed in the Right Hemisphere and those based on Consonant Distinctions are on the Left

Luo et al., 2006, PNAS, 103:19558.

• Distinguishing features in the Mandarin Chinese language can be based on tonality or traditional consonant distinctions.

• MMNs were measured with oddball stimuli changing either the tone or the consonant structure to vary linguistic meaning.

• Source reconstruction of the EP recordings revealed that meaning changes triggered by tonality were stronger in the right hemisphere and those triggered by consonant changes were stronger in the left hemisphere.
Luo et al., 2006
Opposite patterns of hemispheric dominance for early auditory processing of lexical tones and consonants.

Dipole Locations

\[
\begin{align*}
A & \quad x = \pm 45, y = -23, z = 15 \\
B & \quad x = \pm 45, y = -12, z = 10
\end{align*}
\]

Dipole Locations

Tonal Contrast

Consonant Contrast
According to Zatorre (2002), "hemispheric asymmetries in auditory processing (may) arise as a solution to the inherently incompatible requirement that processing of both temporal and spectral information be optimized."
Left and Right Auditory Cortices are Specialized for Stimulus Processing

- Trade-off between accurate temporal and spectral processing is managed by access to two processors.
- Spectral analysis cannot be accurate in short time frames.
- Much of consonant perception, in contrast must occur in short time windows.
Different distribution of Cell Size/Type Across Hemispheres may account for Processing Capacity Differences

Fig. 3. The distribution of cell size from the two hemispheres of one case (012). Cell sizes are largely overlapping, however there are greater numbers of large, magnopyramidal cells in the left hemisphere than the right. From Hutsler, 2003 Brain & Language
“Axon Properties in the Left Hemisphere are responsible for the capacity to process complex temporal patterns.

LH has a greater proportion of fine caliber, slowly conducting axons allowing greater temporal dispersion of any signal, in turn allowing for better capacity for linking the representation of events which are separated in time. Short temporal patterns (such as speech) are thus represented in greater detail and with greater accuracy in the LH than the RH.
The Ear Contralateral to the AC has the same Processing Advantage
Asymmetrical function based on Ear of presentation is also Stimulus-Related

Kimura and colleagues used dichotic stimuli to demonstrate a *slight* but significant right ear advantage for speech perception and a left ear advantage for tonal stimuli (Kimura, 1961) (Kimura, 1964) (King & Kimura, 1972; Kimura, 1973). Subsequent studies validated the finding related to ear performance (Sidtis, 1980; Kallman & Corballis, 1975; Kallman, 1977; Sidtis, 1982).
Dichotic Speech Presentation Shows RE Advantage


Dichotic listening
N = 1466

No of obs

0 2 4 6 8 10 12 14 16 18 20 22 24 26

Right Ear Left Ear

# of Correct Reports of Dichotic CVs
Other Evidence of Asymmetry in the peripheral auditory system.

Is there evidence of Asymmetry from physiologic tests?
Right Ear Amplitude Advantage for Wave V Click-Evoked ABRs from Neonates

Other studies of adult and infant click-evoked ABRs have also shown slight RE advantage. Levine & McGaffigan, 1983; Eldredge & Salamy, 1996.
Asymmetry in Brainstem Responses to Tones

• Studies with much smaller Ns have not shown lateralization of tone burst ABRs in babies.

• The short duration of stimuli used for standard ABR may inhibit the left ear advantage.
Asymmetry Brainstem Responses to Tones

• The Frequency Following Response is a brainstem response elicited with longer duration, low-frequency tones.

• Ballachanda et al. (1994) notes that adult FFR was larger when elicited in the left ear than the right. (JAAA 5:133)
Spontaneous otoacoustic emissions (OAEs) are more prevalent and transient-evoked OAEs are generally larger in right ears than in left.

A click stimulus

Transient Otoacoustic Emission (TEOAE)

Two tonal stimuli

Distortion Product OAE (DPOAE)

Rapid short Clicks

Long duration Tones
OAE SNR in neonates show a pattern of asymmetry that mimics that seen at the level of the auditory cortex, although in the opposite ear. Sininger & Cone-Wesson, Science 2004

Newborns show larger transient evoked emission in the right ear (rapid, short- duration, click stimuli)
OAE SNR in neonates show a pattern of asymmetry that mimics that seen at the level of the auditory cortex, although in the opposite ear. Sininger & Cone-Wesson, Science 2004

and larger tone-evoked otoacoustic emission in left ear.
Human Neonates show a Physiologic Ear Advantage for transient stimuli in the RE and tonal in the Left Ear

Human neonates have VERY immature connections between the ear and auditory cortex!!

Moore et al., 2002

In neonates, at least, the ear advantage may be independent of the cortical processing!
DPOAEs from 6 Children 7-10 Years of Age

DP SNR in dB vs. f2 in Hz

- Red Circle: Right Ear
- Blue Triangle: Left Ear
**What is the mechanism for Stimulus-Related Ear Advantage in Infants??**

Study of 44 neonates investigated two possible mechanisms of ABR asymmetry

Sininger & Cone-Wesson 2006

a) increasing ABR stimulus rate to reveal potential neural conduction and/or synaptic mechanisms

b) using contralateral white noise masking to activate the medial olivocochlear system during click ABRs
Rate Results

• Increasing stimulus rate had the expected result of reducing peak amplitude and increasing peak latency.

• No significant asymmetry was seen in the rate-induced effects.
Does the MOC System Contribute to Ear Asymmetry in Neonates?

50 dB SPL Contralateral White Noise

Amplitude in µV

Milliseconds

Unmasked

Masked

50 dB SPL Contralateral White Noise
Contralateral Masking Reduces Left Ear ABR Amplitude More than Right (P=0.0282)
MOC involvement in Asymmetry

• MOC may be exhibiting asymmetric influence on auditory functions in infants.

• Direction of influence is in line with observed asymmetry: contra noise reduces the click-evoked ABR amplitude more in the left than the right ear, rendering a larger right ear response.

• Currently the only logical explanation for asymmetry of OAEs or ABRs.
Brainstem Mediated Medial Olivo-Cochlear System Modulated Activity of the Outer Hair Cells
Newborn oto-acoustic emission hearing screening tests: Preliminary evidence for a marker of susceptibility to SIDS


Figure 1 Graph demonstrating the right-sided signal to noise ratio differences in 31 SIDS infants versus matched controls.

Found that SIDS infants had lower OAE SNR but ONLY IN THE RIGHT EAR!
“infants with SIDS had a reversal of the usual enhanced TEOAE response in newborns on the right. Signal-to-noise ratios of infants with SIDS consistently trended higher on the left than the right in the 2000–4000 Hz range whereas in the surviving controls the right-sided ratios consistently trended higher than the left.”

“A possible mechanism is that the inner ear may experience a pressure insult from placental transfusion and that this injury may play an important role in the predisposition for SIDS. The fact that a difference in signal to noise ratio was only found on the right side in infants with SIDS may be related to the fact that transfused placental blood moving under pressure through a newborn's veins is likely to be preferentially directed to the veins of the right inner ear.”
Related Questions

• How much difference can we expect to see in the functioning of the two ears based on stimulus type??

• What is the effect of the loss of function in one ear-- how much compensation can be expected??
Study Designed to Examine the Relative Processing Capacity of the Left and Right Ears in Hearing and Unilaterally Deaf Subjects

Participants

• 32 normally-hearing adults (15 F, 17 M)
• Mean age 24.33 y (range 18-39)
• All Right Handed (modified Edinburgh)
• 16 Unilateral Deaf (<age 2):
  9 LE only (7 F)
  7 RE only (5 F)
• Mean age was 26.8 years (SD = 5).
Methods

- **Standard Psychophysics**: frequency discrimination, level discrimination and gap detection using a three-alternative forced choice, 2 down 1 up paradigm with feedback.

- **Electrophysiology Acoustic Change Complexes**: 50% frequency change, 10 dB level change and 20 ms gap.

- Stimuli: **500, 1000 & 4000 Hz** tones and **WBN 50 dB SPL** (1000 omitted in electrophysiology).

- Order of tests and all conditions within test including ear (monaural) were randomized.
Noise Stimuli
Did not show laterality- Responses symmetric!
Experiments should be repeated with a speech-like stimulus that would be expected to show a right ear advantage.
Left Ear Advantage for Level Discrimination of Tones

- Left Ear of Controls shows advantage for level discrim of tones
- Left Ear Unilaterals have an advantage over controls
- Right ear Unilaterals have a disadvantage
Left Ear Advantage for Frequency Discrimination
Left Ear Advantage for Tonal GAP DETECTION but not noise.

No laterality found for gap detection using noise.
Results replicated with a small group of school-aged children. Is there a developmental effect.
Electrophysiology Acoustic Change Complex:
50% frequency change, 10 dB level change and 20 ms gap for 500 & 4000 Hz tones and WBN 50 dB SPL. Acoustic Change Complexes: onset stimulus lasting 700 ms followed by the change. All changes maintained stimulus phase and the intensity change was ramped over 5 ms.

• 64 Channel Recordings using NeuroScan SynAmps2 amplifiers and Neuroscan Electrode Caps.
• EEG was filtered from .1 to 200 Hz
• 200 Averages were used for each condition.
Grand Average Gap Responses at Cz

Left Ear

Right Ear

500 Hz

4000 Hz

White Noise

N1

P2

1 μV
**Grand Average Intensity Change Responses at Cz**

[Graph showing acoustic change responses for different frequencies (500 Hz, 4000 Hz, and white noise) across time (0-1500 ms).]

- **500 Hz**
- **4000 Hz**
- **White Noise**
Grand Average Frequency Change Responses at Cz

Acoustic Change

Time in ms

0 500 1000 1500

Acoustic Change

Time in ms

0 500 1000 1500

4000 Hz

500 Hz
Left Ear Responses are bigger in the contra

Right Ear Responses are slightly bigger in the ipsi

FREQUENCY CHANGE TEMPORAL ELECTRODES

500 Hz

4000 Hz

Time in ms

Ipsilateral Electrodes T7 & TP7
Contralateral Electrodes T8 & TP8

Ipsilateral Electrodes T8 & TP8
Contralateral Electrodes T7 & TP7
**Electrophysiology Results**

**TONES**
When elicited by TONES to the Left Ear, the response from Right Side electrodes is significantly larger.

The Right Ear elicits a symmetrical response.

Left Ear Unilaterals function as expected (good performance).

Right Ear Unilaterals actually process tones primarily on the LEFT SIDE (poor performance).

**NOISE**

Controls show contralateral processing.

Unilaterals process noise on the right side regardless of ear of presentation.
Summary

• General Left Ear Advantage for processing of tonal stimuli.
• Persons with Left Ear Only show advantages in tonal processing even over control subjects.
• Persons with Right Ear Only show no evidence of accommodation and poorer than expected performance on tonal tasks.
• Persons with Right Ear only show disrupted patterns brain activation for tonal and noise stimuli.
• Further study is need to determine laterality of speech processing in unilateral deaf.
• Ear of loss should be considered along with complex processing abilities in evaluation of disability.
References


Thank you for listening.
Gap Detection for Tones is Left Lateralized Noise Shown No Laterality

500 Hz 1000 Hz 4000 Hz WN

Gap Detection Threshold in ms

Left Ear
Right Ear

p = 0.039
ns

Gap Detection in Unilaterally Deaf Subjects

Left Ear
Right Ear

500 Hz 1000 Hz 4000 Hz WN
Music Training Improves Frequency Resolution Capacity
Frequency Resolution Improves and Laterality Diminishes with Years of Music Training

![Graphs showing Frequency Resolution at 500 Hz, 1000 Hz, and 4000 Hz for Left and Right Ear across different years of music training.](image)
Gap Detection Advantage:
Right Ear for Noise-
Gap Detection Advantage:
Left Ear for Tones (4k)
Gap Detection Study

- Type of stimulus had a greater effect on laterality than task.
- There could be some tonal cues in the detection of differences on the GD task.
- The duration of the stimulus (500 ms) may have been insufficient for lateralized processing of 400 Hz.
- Task influence can be seen in smaller laterality effect in LE for tonal stimuli.
Gap Detection- Unilateral Performance

Single Ears of Unilaterally Deaf Perform as Normals
Little or No Compensation for Stimulus-Related Asymmetry
Unilaterally Deaf show little or no evidence of compensation and a disadvantage for processing of broad band stimuli by the lone left ear—this may help to explain poorer performance of RE deaf students in school.

- Twenty-five to 30% of children with UHL will fail at least one grade in school, a rate that is 10 times that of normally hearing peers. Fifty percent of these children require some type of special education/intervention (Bess and Tharpe, 1986; Brookhouser et al., 1994; Klee and Davis-Dansky, 1986; Oyler et al., 1987).
- Teachers of children with UHL have specifically reported difficulty in all areas of academics (Dancer et al., 1995).
- Klee and Davis-Dansky (1986) found verbal IQ in children with RUHL was 9 points lower than those with LUHL.
- RUHL has also been shown to produce more significant disorders of detection of speech in noise Bess F.H., Tharpe A.M., Gibler A.M 1986 and poorer performance on interrupted speech in noise test (Hartvig et al. 1989).
So What?

• Other than concern for those with unilateral deafness, there may be many other applications of this theory.
• Do we need ear-specific processing for hearing aids and cochlear implants?
• Would ear-specific therapies for dyslexia, auditory processing or developmental language disorders be appropriate. (Stuttering, autism, schizophrenia, aphasia)
Further Studies

• Expand the study of auditory processes (tonal discrim, intensity discrim, speech perception in noise) for asymmetry.
• Investigate the lateralization of brain activity for similar functions.
• Continue to investigate unilaterally deaf subjects, early and late onset.
Discussion

• Unilateral ear ablations in non-human mammals results in a reorganization of central projections from the remaining ear showing stronger ipsilateral cortical activation with lower thresholds than is seen in control animals (Kitzes 1984, Reale et al 1987, Popelar et al 1994).


• The subjects in this study are unilaterally deaf since early childhood and this may influence the capacity to reorganize.
Results

Level Discrimination
Left Ear Advantage for Level Discrimination of Tones

![Graph showing level discrimination in dB for different stimuli (500 Hz, 1000 Hz, 4000 Hz, WBN) with data points for left and right ear, and statistical significance p-values of 0.015 and 0.024.]
Left Advantage for Narrow Bandwidths
Sex, Age and Music Influence

Sex: Males consistently show more laterality than Females

Age: Laterality diminishes with Age on Intensity and Frequency tasks but not gap detection.

Music: Performance Increases with Music Training BUT: Laterality increases with music for intensity but decreases with music for frequency discrimination
Thank you for listening.
Specific Parameters

- Minimum Reversals 6
  2 Big Steps (factor of .66)
  Small step (factor of .9)
- One up, two down
- Frequency start: 50 Hz
- Gap start: 100 ms
- Level Start 10 dB
Duration Did Not Influence Laterality

Frequency Resolution Laterality by Duration

all NS
Ear-Specific Acoustic Change Responses

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**Background/Questions**

- We are interested in how and where various stimuli (tones and noise) are processed in the brain and whether stimuli are processed differently depending upon the ear of presentation?

- Last year I reported on how the ear of stimulation influenced psychophysical ability. This year I will discuss the influence of presentation ear and type of stimulus on Cortical Auditory Evoked Potentials used to record changes in intensity, frequency or gap detection?

- How does Ear of Stimulation and Type of Stimulus influence the laterality of dipole sources in the brain.
Three *Auditory “Tasks”* were used:
- Frequency Change- 50% upward change
- Level (Intensity) Change + 10 dB
- Gap Detection 20 ms

Acoustic Change Complexes were made with an onset stimulus lasting 700 ms followed by the change.

All changes maintained stimulus phase and the intensity change was ramped over 5 ms.

Tones of 500 and 4000 Hz were employed for all tasks and broad-band noise was used for gap and level tasks.
When elicited from the Left Ear, the response from Right Side electrodes is significantly larger. The Right Ear elicits a symmetrical response.

**Tones**

Tonal Stimuli, all tasks collapsed
Onset Response

Change Responses

Noise
Asymmetric Processing

• We had hypothesized that tones to the left ear would elicit a robust contra-lateral response in the right hemisphere where spectral processing is enhanced.

• But we also hypothesized that spectrally complex stimuli (noise or speech) would elicit a large contralateral response primarily from the right ear for processing in the Left Hemisphere.

• Only the first hypothesis seems to be verified by our data.
Dipole Source Analysis

To compare the relative strength of activation of the two hemispheres

- Grand Averages were submitted to dipole source modeling assuming two symmetrical dipoles and a 3-shell spherical head model using Neuroscan “Source” software.

- N1 activity for Onset and Acoustic Change activity was evaluated for a 50 ms window surrounding the peak of the Global Field Power.

- Dipole location was indicated in mm in the X, Y and Z planes and dipole source strength was indicated in nAmp.
Dipole Strength Comparison for Left/Right Hemisphere

- **Closed Circle LE**
- **Open Triangel RE**
- **Blue/Cyan 4000 Hz**
- **Pink/Red 500 Hz**
- **Green/Green Noise**
Dipole Strength Comparison by Hemisphere

Stimuli

<Left Hemisphere Advantage

<Right Hemisphere Advantage

Intensity Onset

Onset

Frequency

LE Onset

LE Change

RE Onset

RE Change

Stimuli

-500 - 4000 - WN - 500 - 4000 - WN

0

10

20 nAm
2010 Results: Gap Detection and Level Discrimination for tones better in the left ear.
Discussion/Conclusions

- Left Ear Stimulation leads to a strong right hemisphere activation.
- Spectral analysis and tonal processing is facilitated in the right hemisphere.
- The electrophysiologic results help to explain the preferential performance of the left ear in the psychophysical responses.

Questions Raised

- Why do noise stimuli act in a similar fashion to tones?
- Will more temporally complex stimuli give a similar right ear advantage and left hemisphere response?
- How will persons with unilateral deafness respond?
Thank you for listening.
Processing consequences of unilateral deafness - implications for screening

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2) David Geffen School of Medicine at UCLA, Department of Head & Neck Surgery,
   Los Angeles, California, USA
3) Laboratoire Psychologie de la Perception, CNRS, Université Paris Descartes, France
Screening for Unilateral Hearing Loss is Controversial

• Consequences of Unilateral Hearing Loss are elusive but evidence includes
  – Significant Language and Educational delays
  – Evidence of impaired localization
  – Difficulty for hearing in noise.

• The human auditory system is meant to be bilateral. The fully functioning system has dual processors to manage the demands of real time auditory stimuli.
Based on brain scans and cell type analysis we know that *Spectral Processing* is maximized in the *RIGHT* temporal areas and *Rapid Temporal Processing* is best performed in the *left* hemisphere.

Zatorre & Belin 2001

Auditory processing areas of the left and right cortical hemispheres have differential processing capacity to maximize the *simultaneous processing of spectral and temporal information.*
The Ear Contralateral to the AC has the same Processing Advantage

Right

Spectral Processor

Left

Rapid Temporal Processor
Questions re Unilateral Hearing Loss

• What Happens to the Processing Capacity of the Child with One Ear functioning alone?
• Does it matter if the remaining ear is Right or Left?
• Is there any reorganization or compensation for the temporal or spectral processing that would have been provided by the contralateral ear?
Study Designed to Examine the Relative Processing Capacity of the Left and Right Ears in Hearing and Unilaterally Deaf Subjects

Participants

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- Mean age 24.33 y (range 18-39)
- All Right Handed (modified Edinburgh)
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- Mean age was 26.8 years (SD = 5).
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• EEG was filtered from .1 to 200 Hz.
Grand Average Recordings

LEFT EAR

RIGHT EAR

FREQUENCY

MIDLINE CZ

IPSI LEFT

CONTRALATERAL

IPSI RIGHT

500 Hz

4000 Hz

1 \mu V

0 200 400 600 800 1000 1200
Electrophysiology Results

When elicited by TONES to the Left Ear, the response from Right Side electrodes is significantly larger. The Right Ear elicits a symmetrical response.

Left Ear Unilaterals function as expected (good performance). Right Ear Unilaterals actually process tones primarily on the LEFT SIDE (poor performance).

Controls show contralateral processing. Unilaterals process noise on the right side regardless of ear of presentation.

TONES

NOISE

Amplitude in $\mu V$

LE  RE  LE  RE

LE  RE  LE  RE

Right Side Electrodes
Left Side Electrodes
Summary

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• Ear of loss should be considered along with complex processing abilities in evaluation of disability.
References


To add to the understanding of the consequences of unilateral deafness, this investigation asked whether early-onset, unilateral deafness and the side of deafness influence natural hemispheric laterality of auditory system cortical activity. **Methods:** subjects were 22 right handed, young adults with normal hearing in both ears (controls) and 12 unilaterally-deaf experimental subjects. Cortical Evoked Potentials were used to record Acoustic change complexes from 64 channels using NeuroScan SynAmps2 amplifiers and NeuroScan Electrode Caps. Stimulus change conditions included frequency (50% upward change) level (+ 10 dB change) and silent gap (20 ms). Tones of 500 and 4000 Hz were employed for all tasks and broad-band noise was used for gap and level tasks. Analysis of onset and change responses included latency and amplitude measures for N100. **Results—Controls:** Tonal stimuli when presented to the left ear reveal larger responses from contra-lateral (right side) electrodes while tones to the right ear consistently shows a symmetrical response. The overall effect is for a predominant right hemisphere response for tonal stimuli. When noise is used both ears demonstrate a larger contra-lateral response. **Unilateral—** For tonal stimuli the contra-lateral response was greater for both left and right ears but for noise stimuli the response is greater from the right side electrodes regardless of ear. Thus, tonal processing of Left Ear Only subjects is similar to controls and shows enhanced Right Hemisphere activation but Right Ear Only subjects demonstrate a Left Hemisphere activation to tones (as opposed to a symmetric response seen in controls). **Discussion** Based on hemispheric specialization of processing, children with hearing only in the right ear may be disadvantaged for processing of tonal stimuli.