From Tones to Speech: Cortical Representations and Exposure Guided Plasticity in Auditory Cortex

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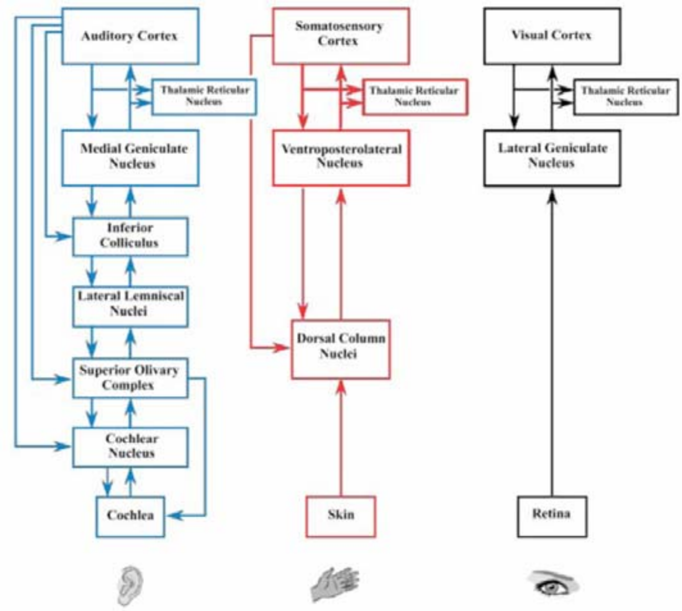
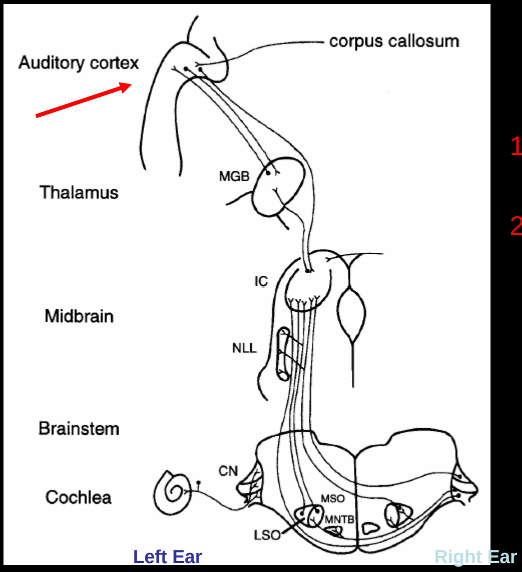
KEY QUESTIONS

- How is information represented in the brain?
- How does sensory input direct change in cortical networks?



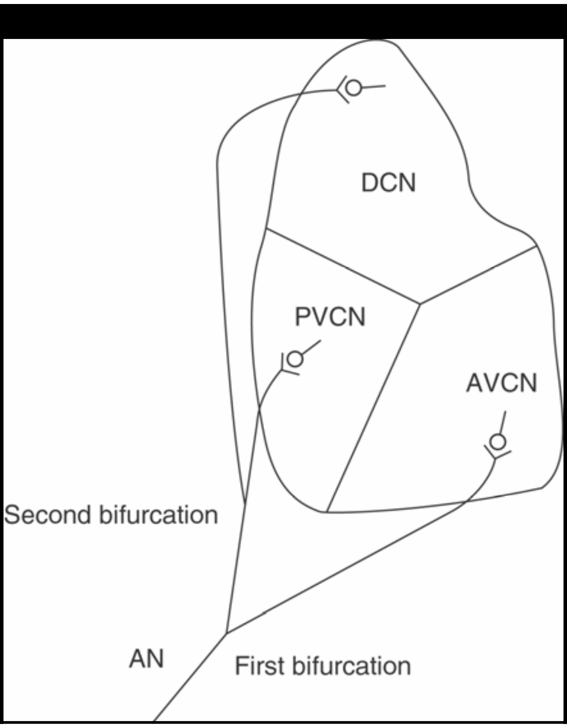
What is unique about the auditory system?



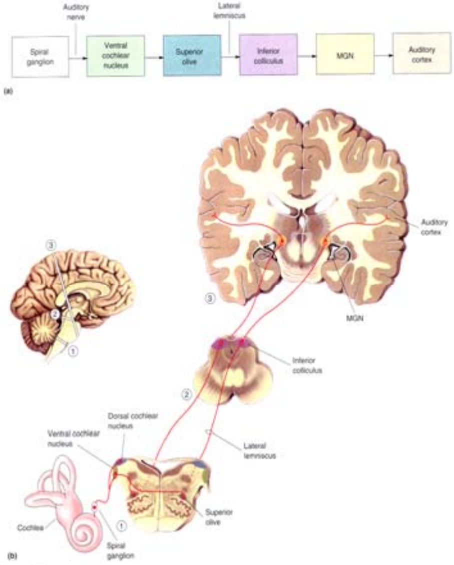
1. Long subcortical pathway
2. Time is an essential axis

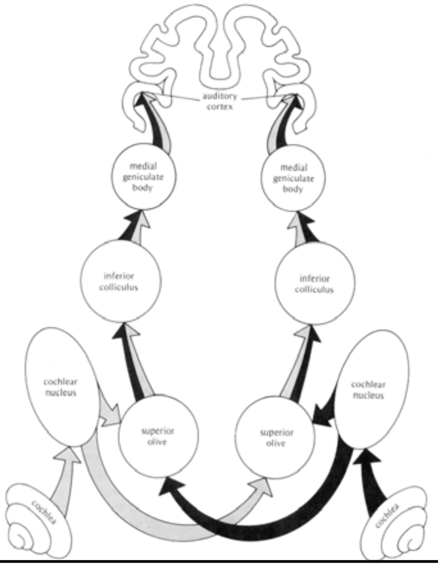
Two bifurcations of the auditory nerve fibers

BEGIN PARALLEL PROCESSING!

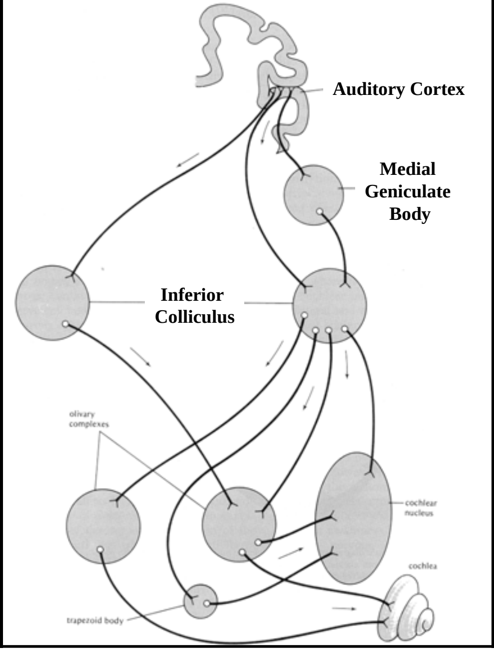


Classical Ascending Auditory System





Descending Pathways



- Corticofugal system
- Olivocochlear system

Auditory Cortex has a Parallel-Hierarchical Organization

Classical auditory pathways

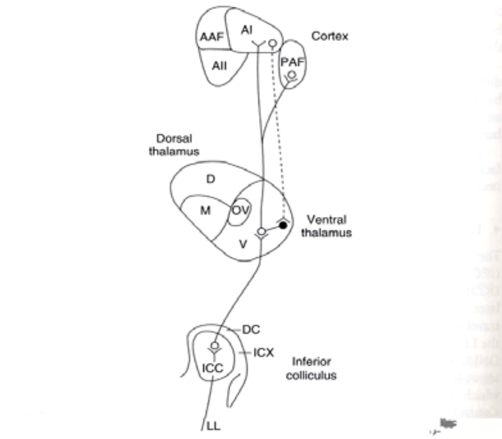
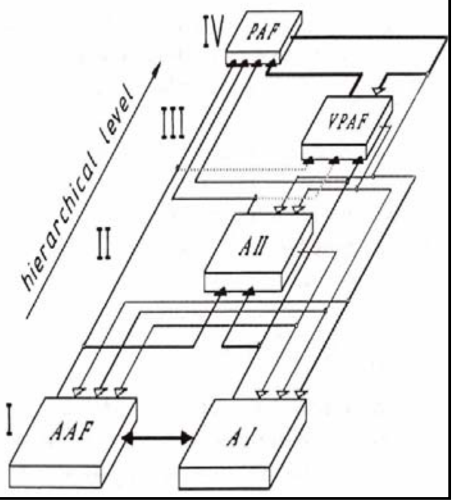


FIGURE 5.27 Schematic drawing of the ascending pathways from the central nucleus of the inferior colliculus (ICC) to the ventral portion of the thalamus and their connections to auditory cortical radiations. Most of the connections have reciprocal descending connections, only one of which is shown (between AI and the thalamus). M, medial (or magnocellular) division of thalamus; D, dorsal division; V, ventral division, OV, ovoid part of the thalamus.

Hierarchical arrangement of cortical fields in cat

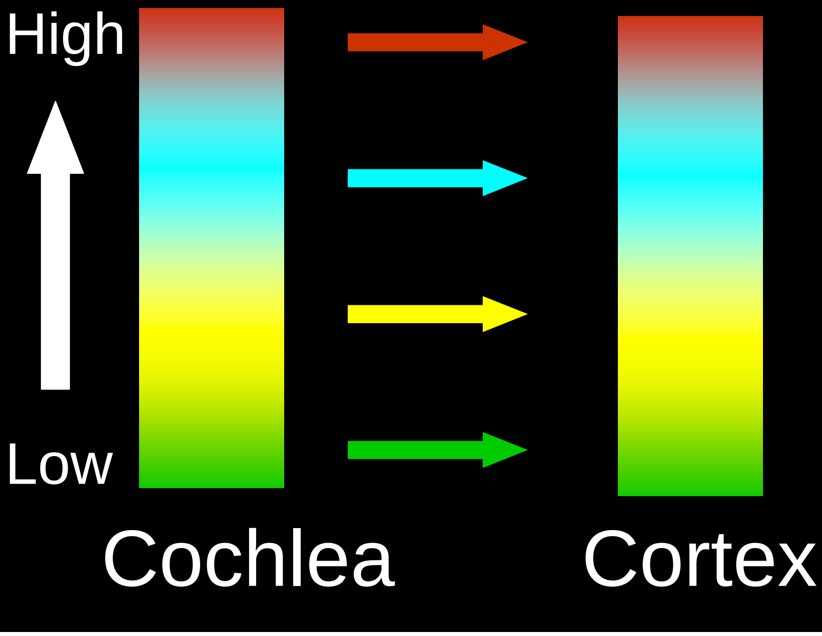


OUTLINE:

1) Cortical responses to simple and complex sound patterns

2) Tone and complex sound exposure alters spectral selectivity of auditory cortex neurons

3) Acoustic context shapes the expression of cortical plasticity

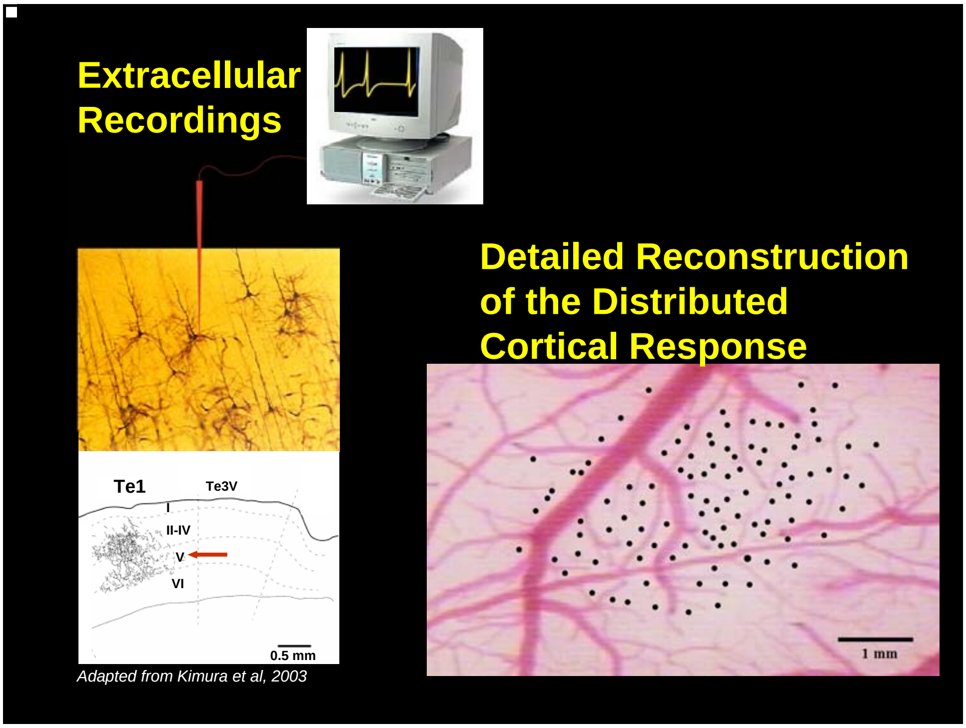


High

Low

Cochlea

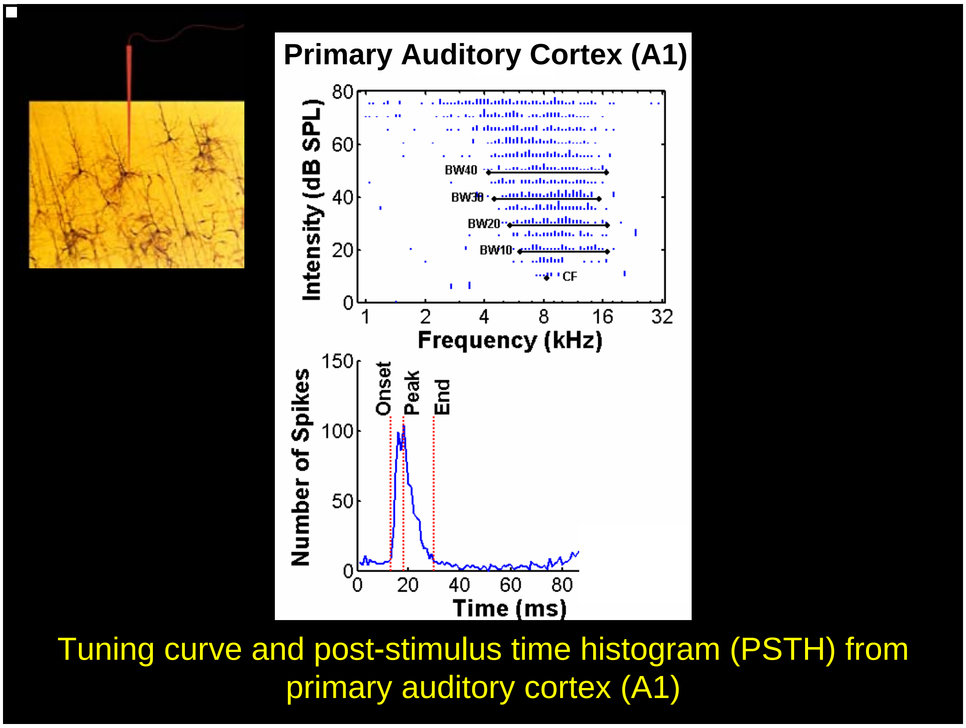
Cortex



Extracellular Recordings

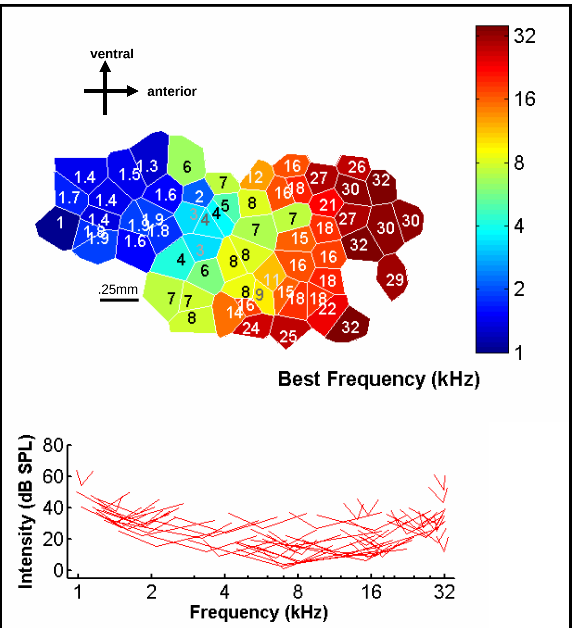
Detailed Reconstruction of the Distributed Cortical Response

Adapted from Kimura et al, 2003



Primary Auditory Cortex (A1)

Tuning curve and post-stimulus time histogram (PSTH) from primary auditory cortex (A1)



Best frequency map and tuning curve tips of primary auditory cortex (A1) from an adult subject

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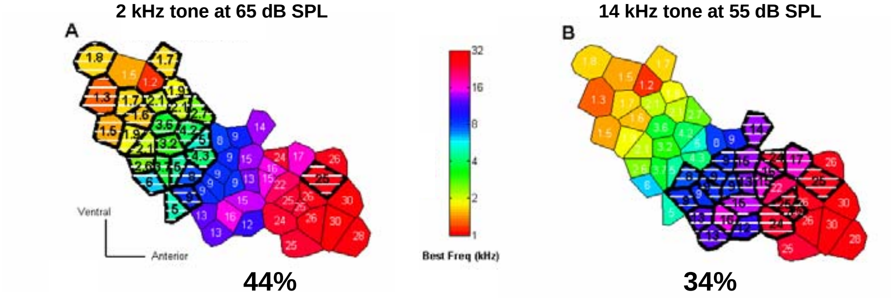
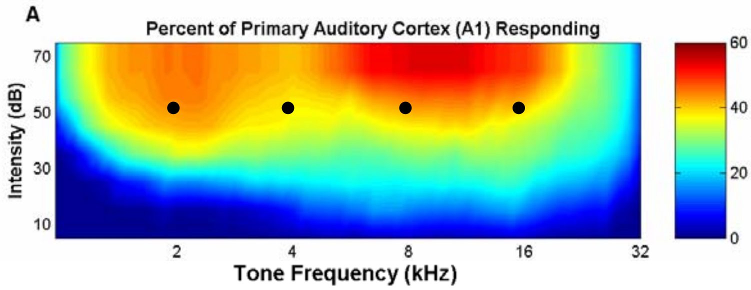


2 kHz tone at 65 dB SPL **44%**

14 kHz tone at 55 dB SPL **34%**

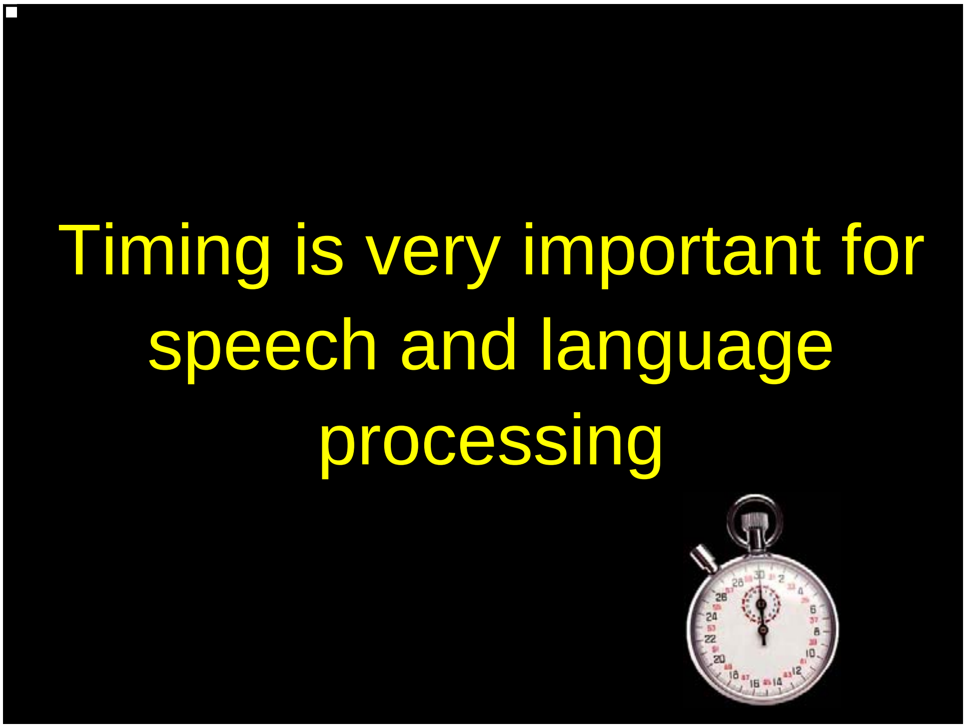
Figure. Best frequency map of primary auditory cortex (A1) from a naïve control adult rat to 2 kHz (Panel A) and 14 kHz (Panel B) suprathreshold tones



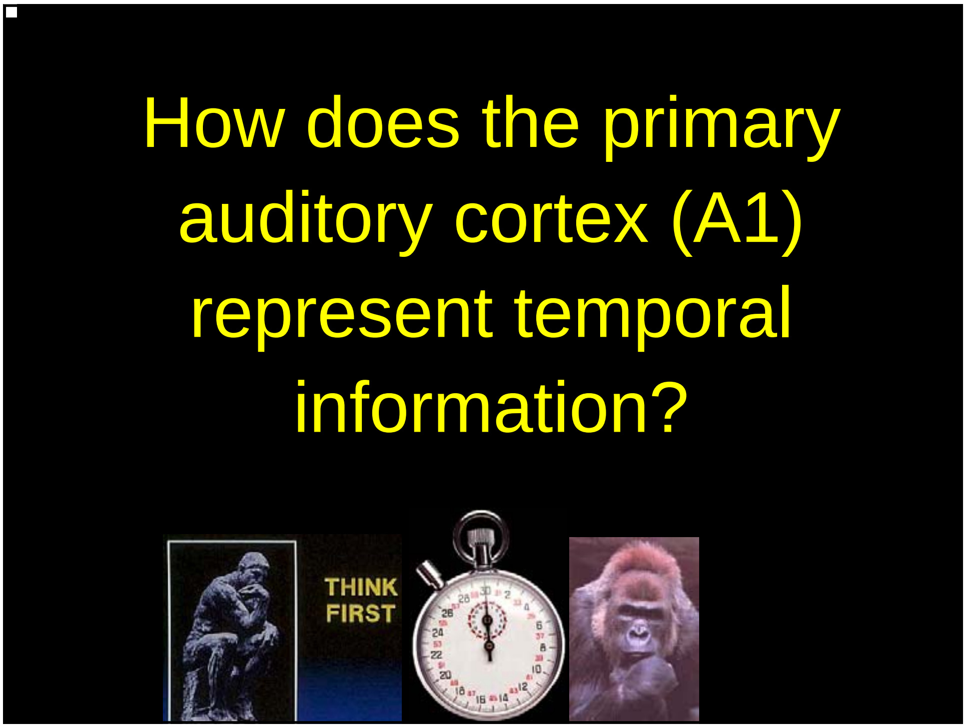
- 2 kHz @ 50 dB SPL: 41% ± 2
- 4 kHz @ 50 dB SPL: 36% ± 2
- 8 kHz @ 50 dB SPL: 38% ± 2
- 16 kHz @ 50 dB SPL: 34% ± 2

Figure. Average percent of the surface of primary auditory cortex (A1) responding to tones (n=15 rats)

Adapted from Pandya et al, Hearing Research (2005)

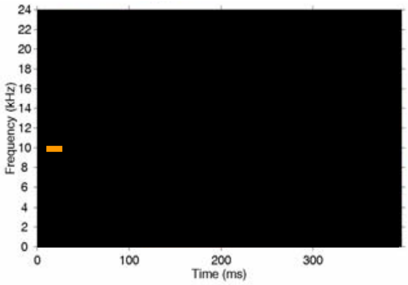


Timing is very important for speech and language processing

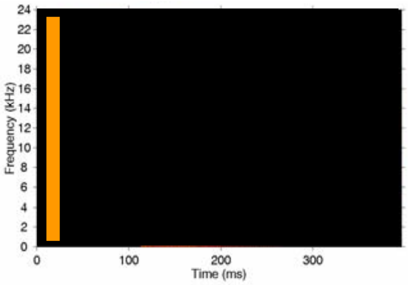


How does the primary auditory cortex (A1) represent temporal information?

SIMPLE INPUT

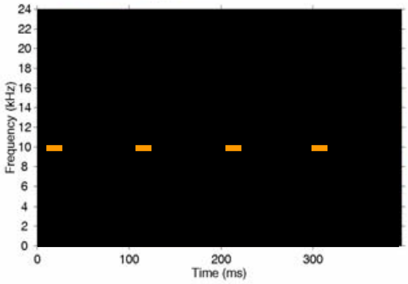


Tone

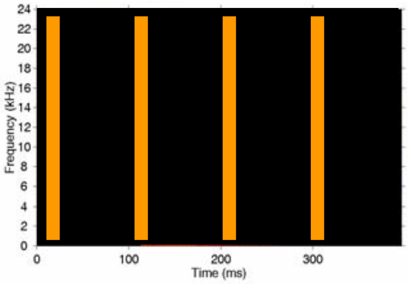


Noise Burst

SIMPLE INPUT PATTERNS

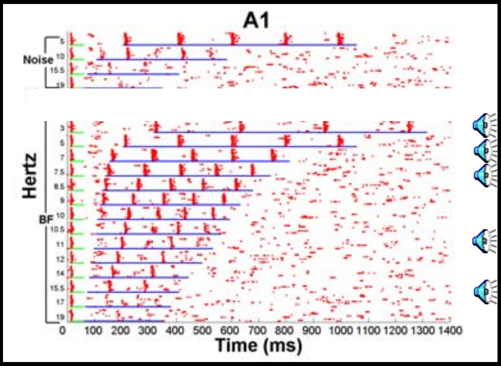


Tone Train



Noise Burst Train

A1 Response to Tone and Noise Trains

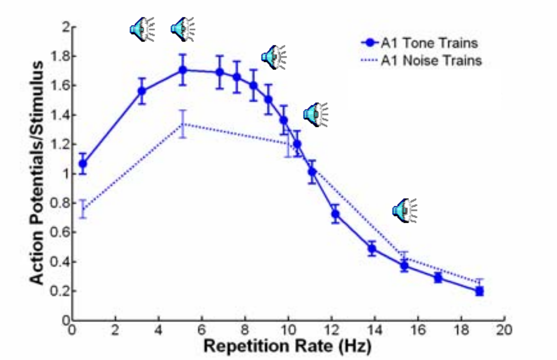


- Response of Individual Site in A1 to Repeated Tones or Noise

Pandya et al, Cerebral Cortex 2007

Neural Response of A1 to Tone Trains and Noise Trains

Group Data



- Average response significantly decreased at rates above ~10 Hz
- Temporal acoustic context matters!

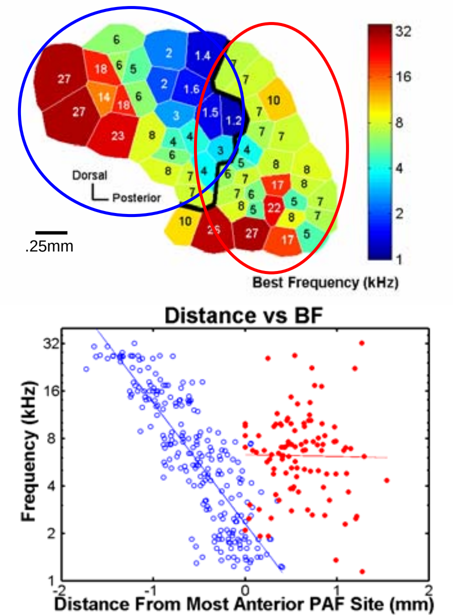
Pandya et al, Cerebral Cortex 2007

PUNCHLINE: Neurons are filters for **frequency** and **time**!

Other cortical fields differ from primary auditory cortex

- Spectral & temporal processing in the posterior auditory field (PAF)

Primary vs. Posterior Auditory Field

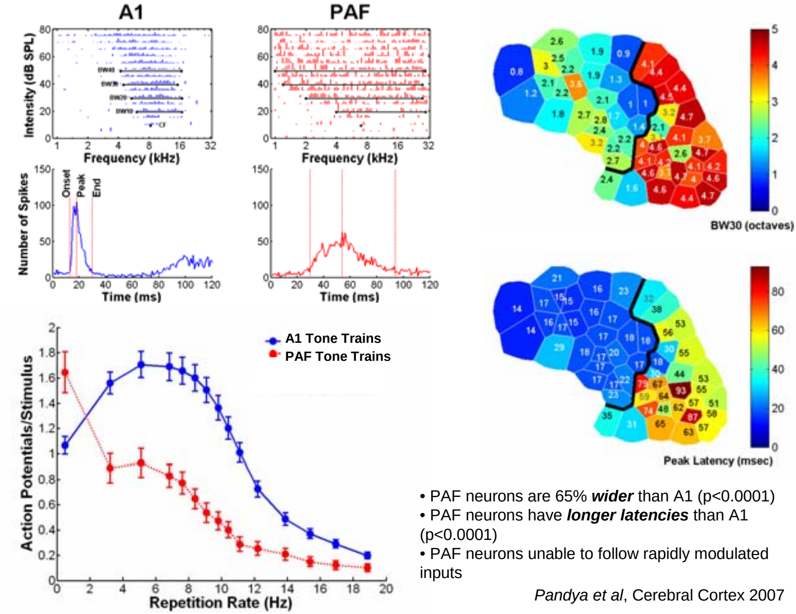


- Map of best frequency of A1 & PAF from an individual rat

- Group data – strong tonotopic organization in A1 but little evidence in PAF

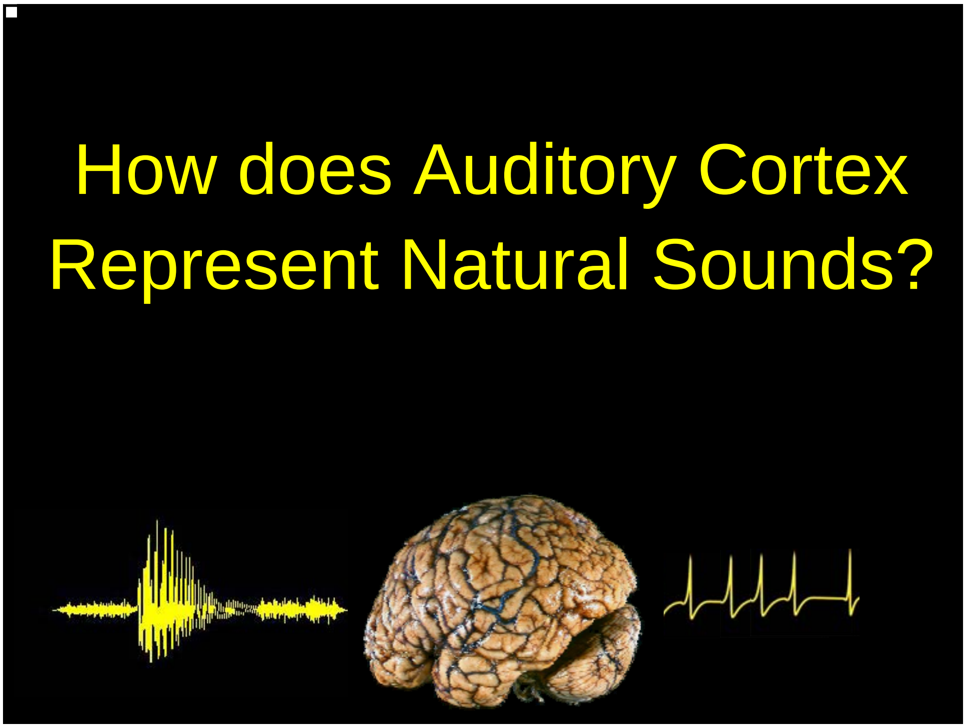
Pandya et al, Cerebral Cortex 2007

Primary vs. Posterior Auditory Field

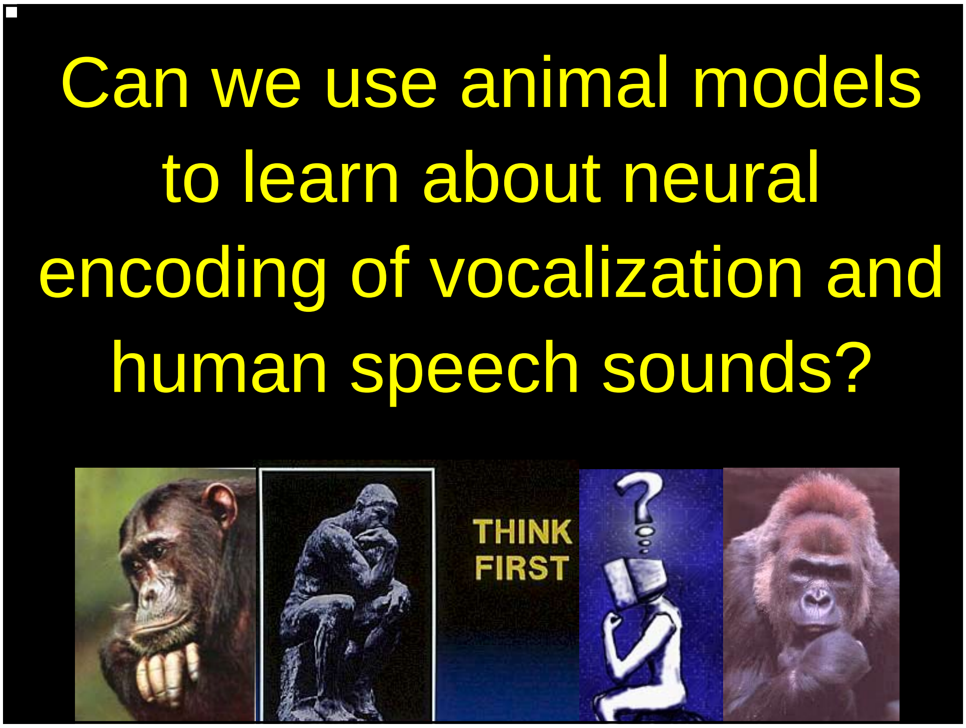


- PAF neurons are 65% ***wider*** than A1 (p<0.0001)
- PAF neurons have ***longer latencies*** than A1 (p<0.0001)
- PAF neurons unable to follow rapidly modulated inputs

Pandya et al, Cerebral Cortex 2007



How does Auditory Cortex Represent Natural Sounds?



Can we use animal models to learn about neural encoding of vocalization and human speech sounds?

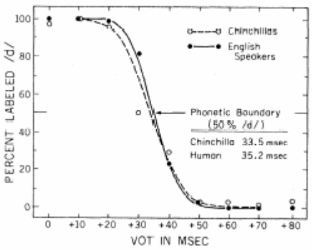


Fig. 2. Mean percentage of /d/ responses by chinchilla and human subjects to synthetic speech sounds constructed to approximate /ta/ and /da/. The animals were trained (that is, given appropriate feedback) on the two "endpoint" stimuli, VOT's of 0 and +80 msec; for all other stimuli (VOT's from +10 to +70 msec in 10-msec steps), feedback was arranged to indicate a correct response to the animal. The labeling gradients and "phonetic boundaries" for human and chinchilla subjects are similar.

- Behavioral Training Generalized
- 'Phonetic Boundaries' for chinchillas and English speaking adults were similar

Speech Perception by the Chinchilla: Voiced-Voiceless Distinction in Alveolar Plosive Consonants

Patricia K. Kuhl; James D. Miller

Science, Vol. 190, No. 4209. (Oct. 3, 1975), pp. 69-72.

What does this tell us?

- Nonhuman animals can discriminate speech contrasts
- Animals can respond to speech 'categorically'
- Animals demonstrate 'categorical perception' to voicing and place **features** of speech sounds

IS SPEECH SPECIAL?

Do we know anything about the neural coding and representation of speech sounds?

[YES]

AUDITORY NERVE

FIRING RATE AND
‘NEURAL SYNCHRONY’
NEED TO BE
CONSIDERED

Young ED, Sachs MB. Representation of steady-state vowels in the temporal aspects of the discharge patterns of populations of auditory-nerve fibers.
J Acoust Soc Am. 1979 Nov;66(5):1381-1403.

Sachs MB, Young ED. Encoding of steady-state vowels in the auditory nerve: representation in terms of discharge rate.
J Acoust Soc Am. 1979 Aug;66(2):470-9.

AUDITORY NERVE

Delgutte B, Kiang NY. Speech coding in the auditory nerve: V. Vowels in background noise.
J Acoust Soc Am. 1984 Mar;75(3):908-18.

Delgutte B, Kiang NY. Speech coding in the auditory nerve: IV. Sounds with consonant-like dynamic characteristics.
J Acoust Soc Am. 1984 Mar;75(3):897-907.

Delgutte B, Kiang NY. Speech coding in the auditory nerve: III. Voiceless fricative consonants.
J Acoust Soc Am. 1984 Mar;75(3):887-96.

Delgutte B, Kiang NY. Speech coding in the auditory nerve: I. Vowel-like sounds.
J Acoust Soc Am. 1984 Mar;75(3):866-78.

AUDITORY NERVE

Sinex DG, McDonald LP. Synchronized discharge rate representation of voice-onset time in the chinchilla auditory nerve.
J Acoust Soc Am. 1989 May;85(5):1995-2004.

Sinex DG, McDonald LP. Average discharge rate representation of voice onset time in the chinchilla auditory nerve.
J Acoust Soc Am. 1988 May;83(5):1817-27.

Sinex DG, Geisler CD. Responses of auditory-nerve fibers to consonant-vowel syllables.
J Acoust Soc Am. 1983 Feb;73(2):602-15.

NEUROSCIENCE AND CLINICAL IMPLICATIONS

Sachs MB, Bruce IC, Miller RL, Young ED. Biological basis of hearing-aid design.
Ann Biomed Eng. 2002 Feb;30(2):157-68.

Schilling JR, Miller RL, Sachs MB, Young ED. Frequency-shaped amplification changes the neural representation of speech with noise-induced hearing loss. Hear Res. 1998 Mar;117(1-2):57-70.

Sachs MB, Young ED, Miller MI. Speech encoding in the auditory nerve: implications for cochlear implants. Ann N Y Acad Sci. 1983;405:94-113.

NEUROSCIENCE AND CLINICAL IMPLICATIONS

Kiang NY, Eddington DK, Delgutte B. Fundamental considerations in designing auditory implants.
Acta Otolaryngol. 1979 Mar-Apr;87(3-4):204-18.

Do we know much about the neural coding and representation of speech sounds at other levels?

[YES – but not much…]

AUDITORY CORTEX – primate

Steinschneider M, Fishman YI, Arezzo JC. Representation of the voice onset time (VOT) speech parameter in population responses within primary auditory cortex of the awake monkey.
J Acoust Soc Am. 2003 Jul;114(1):307-21.

Steinschneider M, Volkov IO, Noh MD, Garell PC, Howard MA 3rd. Temporal encoding of the voice onset time phonetic parameter by field potentials recorded directly from human auditory cortex.
J Neurophysiol. 1999 Nov;82(5):2346-57.

Steinschneider M, Schroeder CE, Arezzo JC, Vaughan HG Jr. Physiologic correlates of the voice onset time boundary in primary auditory cortex (A1) of the awake monkey: temporal response patterns.
Brain Lang. 1995 Mar;48(3):326-40.

Steinschneider M, Schroeder CE, Arezzo JC, Vaughan HG Jr. Speech-evoked activity in primary auditory cortex: effects of voice onset time. Electroencephalogr Clin Neurophysiol. 1994 Jan;92(1):30-43.

AUDITORY CORTEX - cat

Only the /ba/ - /pa/
continuum was tested

Eggermont JJ. Representation of a voice onset time continuum in primary auditory cortex of the cat.
J Acoust Soc Am. 1995 Aug;98(2 Pt 1):911-20.

Advantages of the Rat

- Extensive behavioral studies
  - frequency discrimination, gap detection, modulation rate detection, etc.
- Techniques appropriate for many levels of analysis
  - molecular, cellular, systems, and behavioral

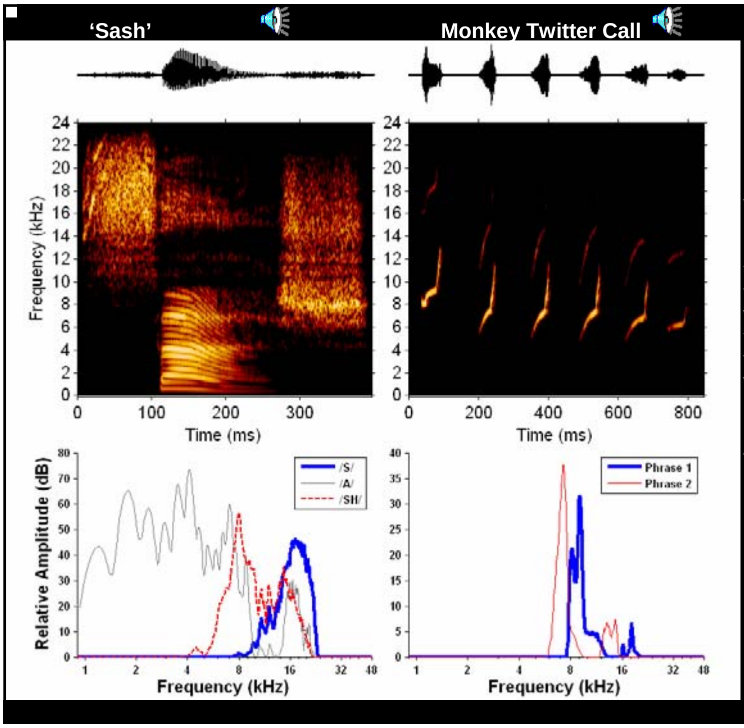
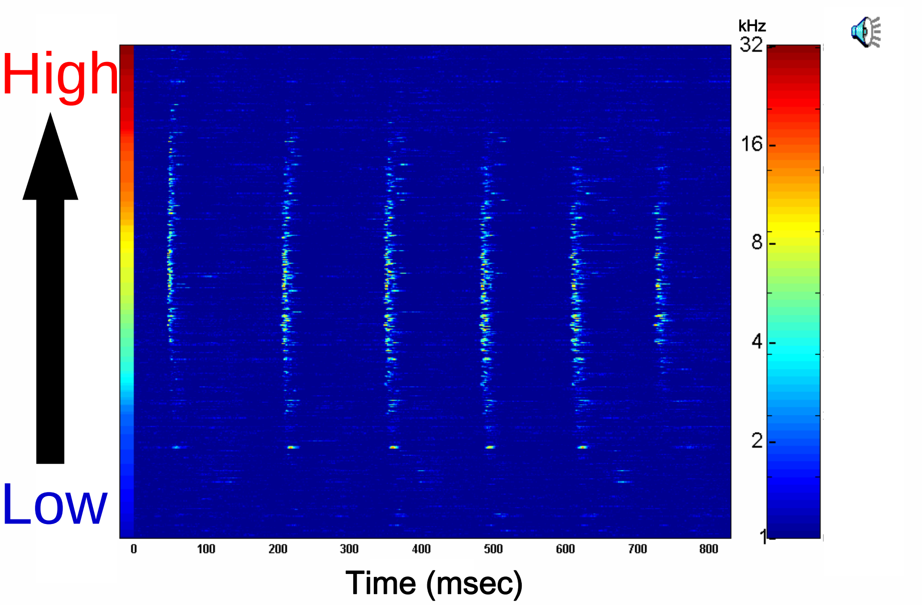
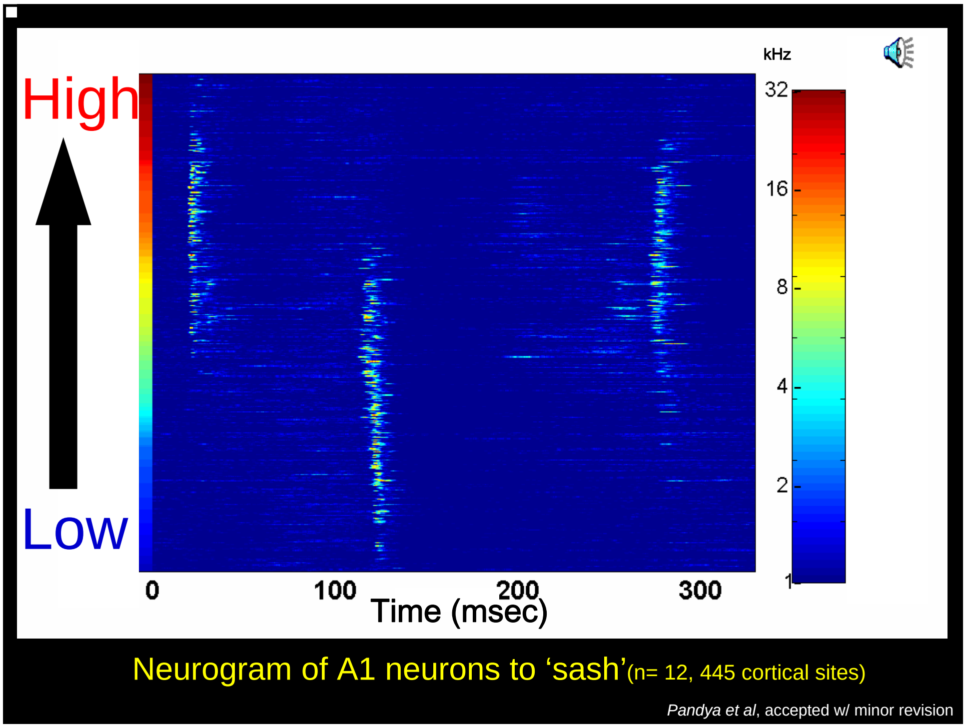


Figure. Time-domain waveforms (top) and spectrograms (middle) showing changes in frequency content as a function of time for the word /SASH/ (left) and the marmoset twitter vocalization (right) that were used as stimuli. The power spectra of the three elements of the word /SASH/ and the first two phrases of the twitter call are provided below the each spectrogram, respectively.



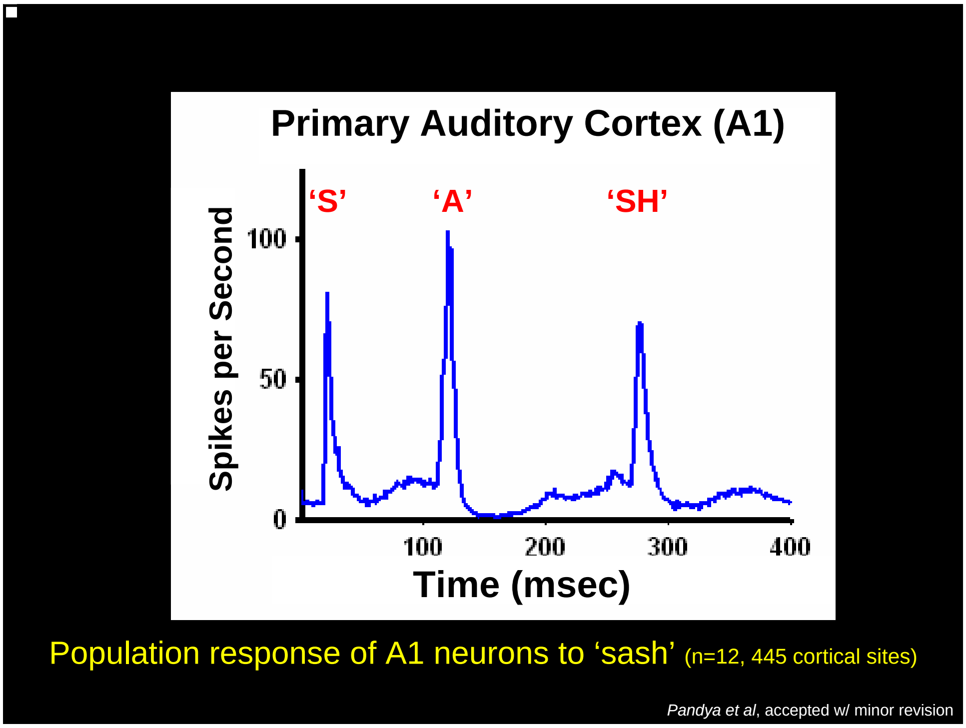
Neurogram of A1 neurons to 'twitter'(n= 12, 445 cortical sites)

Pandya et al, accepted w/ minor revision



Neurogram of A1 neurons to ‘sash’(n= 12, 445 cortical sites)

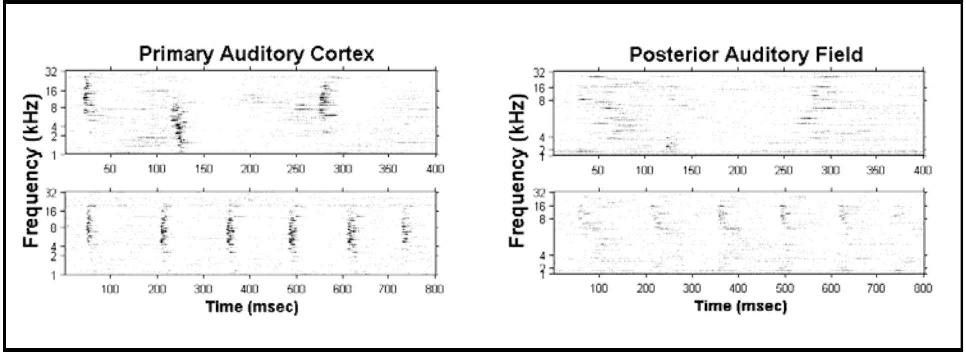
Pandya et al, accepted w/ minor revision



Population response of A1 neurons to ‘sash’ (n=12, 445 cortical sites)

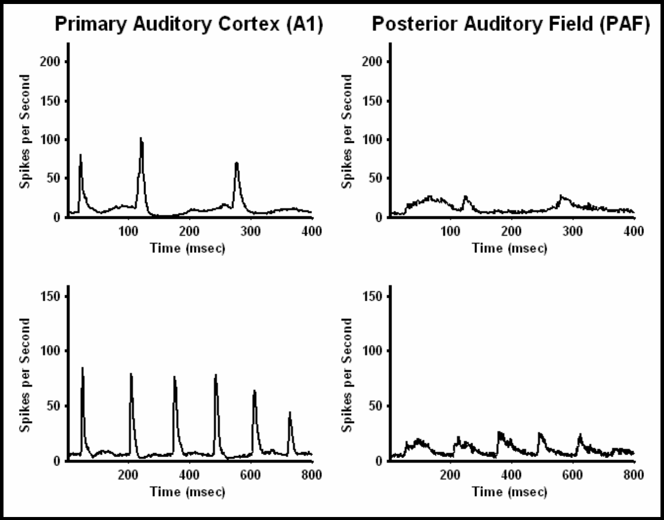
Pandya et al, accepted w/ minor revision

Primary vs. Posterior Auditory Field



Pandya et al, accepted w/ minor revision

Primary vs. Posterior Auditory Field



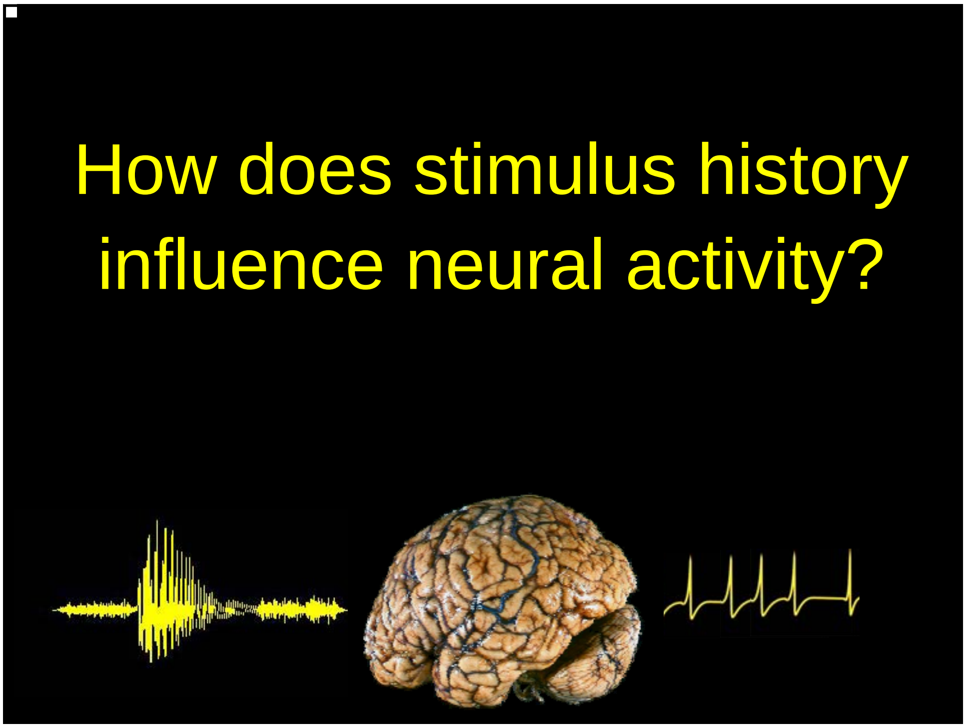
(A1: n=12 rats, 445 sites)

(PAF: n=8 rats, 179 sites)

Pandya et al, accepted w/ minor revision

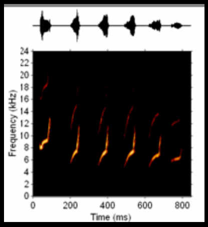
Forward Masking

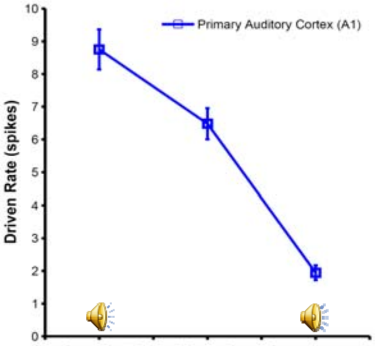
- Psychophysical: the deterioration in performance caused by a masker preceding the signal
- Physiological: the deterioration of a response caused by a preceding signal element

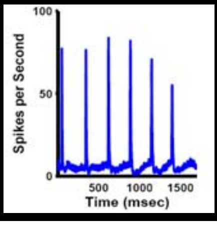


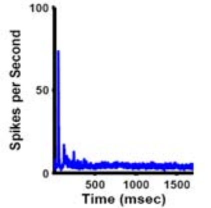
How does stimulus history influence neural activity?

Temporal Manipulations of Monkey Call



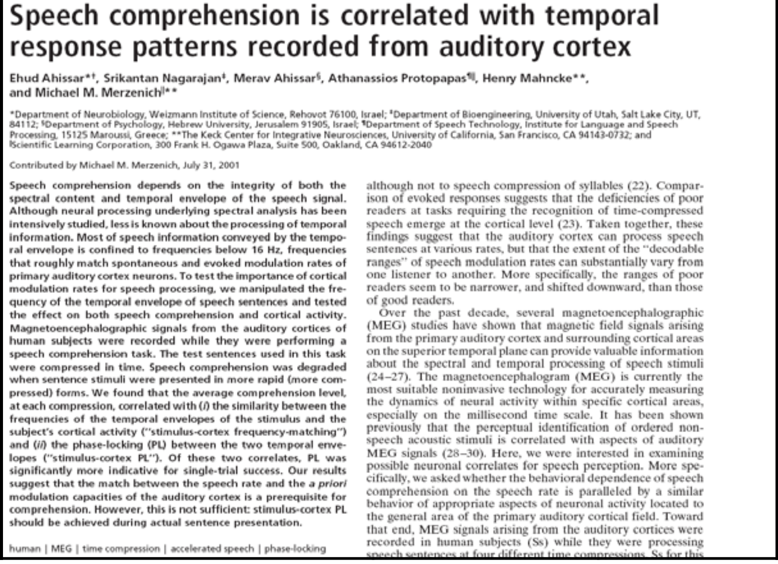






Adapted from Pandya et al, in review

Relevance to Psychophysical and Neuroimaging Studies in Humans



Speech comprehension is correlated with temporal response patterns recorded from auditory cortex

Ehud Ahissar[*][†], Srikantan Nagarajan[‡], Merav Ahissar[§], Athanassios Protopapas[¶][‖], Henry Mahncke[**], and Michael M. Merzenich[‖][**]

[*]Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel; [‡]Department of Bioengineering, University of Utah, Salt Lake City, UT, 84112; [§]Department of Psychology, Hebrew University, Jerusalem 91905, Israel; [¶]Department of Speech Technology, Institute for Language and Speech Processing, 15125 Maroussi, Greece; [**]The Keck Center for Integrative Neurosciences, University of California, San Francisco, CA 94143-0732; and [‖]Scientific Learning Corporation, 300 Frank H. Ogawa Plaza, Suite 500, Oakland, CA 94612-2040

Contributed by Michael M. Merzenich, July 31, 2001

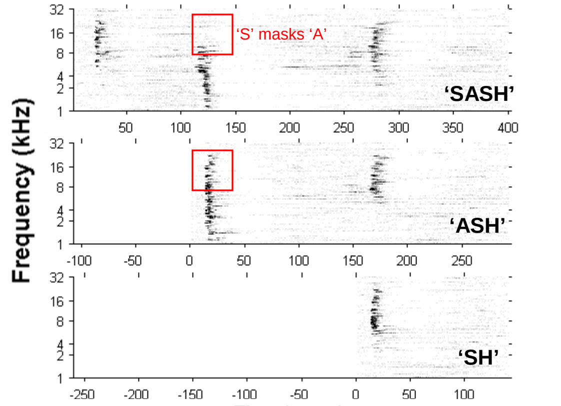
Speech comprehension depends on the integrity of both the spectral content and temporal envelope of the speech signal. Although neural processing underlying spectral analysis has been intensively studied, less is known about the processing of temporal information. Most of speech information conveyed by the temporal envelope is confined to frequencies below 16 Hz, frequencies that roughly match spontaneous and evoked modulation rates of primary auditory cortex neurons. To test the importance of cortical modulation rates for speech processing, we manipulated the frequency of the temporal envelope of speech sentences and tested the effect on both speech comprehension and cortical activity. Magnetoencephalographic signals from the auditory cortices of human subjects were recorded while they were performing a speech comprehension task. The test sentences used in this task were compressed in time. Speech comprehension was degraded when sentence stimuli were presented in more rapid (more compressed) forms. We found that the average comprehension level, at each compression, correlated with (*i*) the similarity between the frequencies of the temporal envelopes of the stimulus and the subject's cortical activity ("stimulus-cortex frequency-matching") and (*ii*) the phase-locking (PL) between the two temporal envelopes ("stimulus-cortex PL"). Of these two correlates, PL was significantly more indicative for single-trial success. Our results suggest that the match between the speech rate and the *a priori* modulation capacities of the auditory cortex is a prerequisite for comprehension. However, this is not sufficient: stimulus-cortex PL should be achieved during actual sentence presentation.

human | MEG | time compression | accelerated speech | phase-locking

although not to speech compression of syllables (22). Comparison of evoked responses suggests that the deficiencies of poor readers at tasks requiring the recognition of time-compressed speech emerge at the cortical level (23). Taken together, these findings suggest that the auditory cortex can process speech sentences at various rates, but that the extent of the "decodable ranges" of speech modulation rates can substantially vary from one listener to another. More specifically, the ranges of poor readers seem to be narrower, and shifted downward, than those of good readers.

Over the past decade, several magnetoencephalographic (MEG) studies have shown that magnetic field signals arising from the primary auditory cortex and surrounding cortical areas on the superior temporal plane can provide valuable information about the spectral and temporal processing of speech stimuli (24–27). The magnetoencephalogram (MEG) is currently the most suitable noninvasive technology for accurately measuring the dynamics of neural activity within specific cortical areas, especially on the millisecond time scale. It has been shown previously that the perceptual identification of ordered nonspeech acoustic stimuli is correlated with aspects of auditory MEG signals (28–30). Here, we were interested in examining possible neuronal correlates for speech perception. More specifically, we asked whether the behavioral dependence of speech comprehension on the speech rate is paralleled by a similar behavior of appropriate aspects of neuronal activity located to the general area of the primary auditory cortical field. Toward that end, MEG signals arising from the auditory cortices were recorded in human subjects (Ss) while they were processing speech sentences at four different time compressions. Ss for this

Naïve Controls (A1)

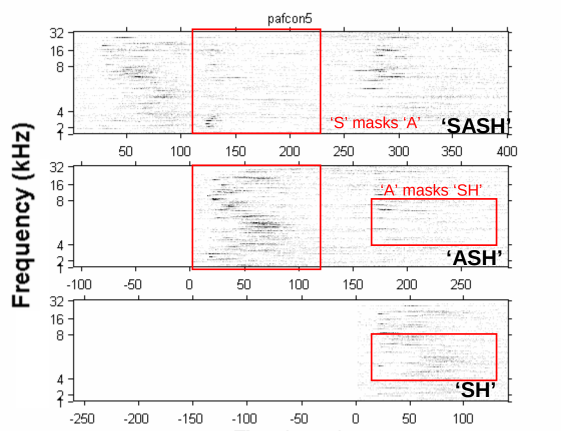


- Neurons between 6-24 kHz respond to /A/ with fewer spikes when preceded by /S/ compared to when in isolation
- Low frequency neurons were unaffected
- Neurons between 4-20 kHz show no masking of /SH/ when preceded by /A/ or /SA/

Neurogram of A1 control neurons to 'sash', 'ash', 'sh'
(n= 12, 445 cortical sites)

Pandya et al, in prep

Naïve Controls (PAF)



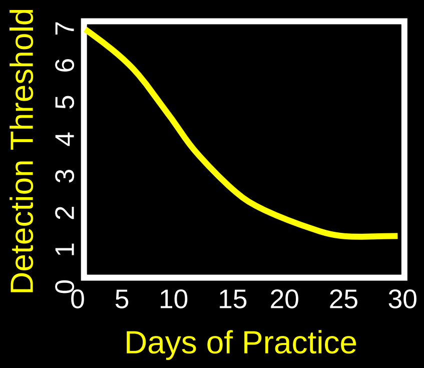
- /A/ preceded by /S/ shows 72% suppression

caxis([0 400])

Neurogram of PAF neurons to 'sash', 'ash', 'sh'
(n= 8, 179 cortical sites)

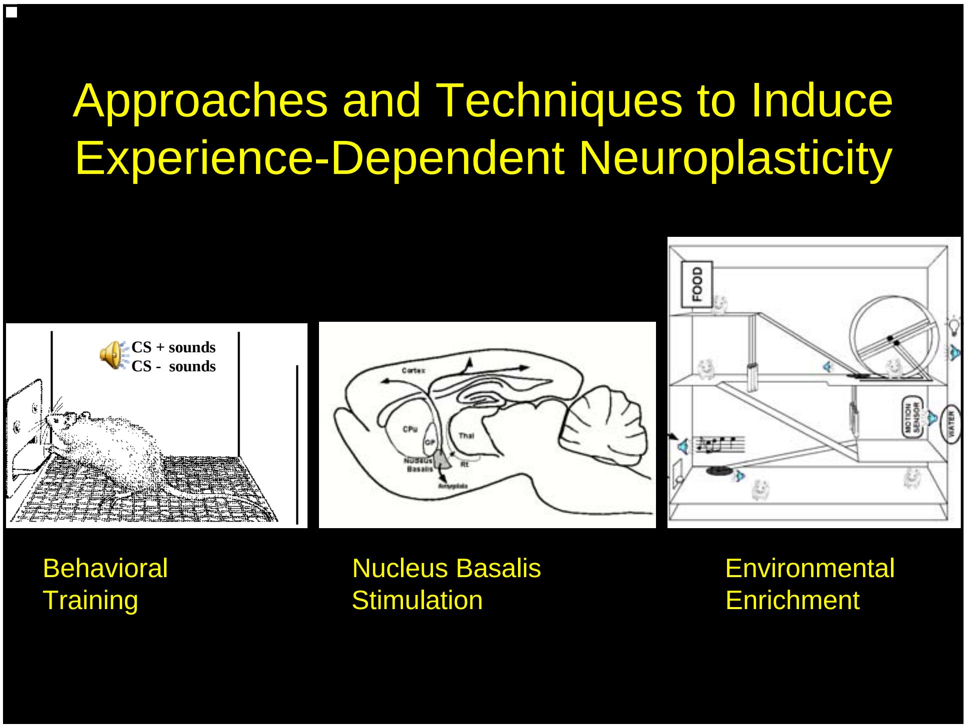
How does plasticity alter neural coding and cortical organization?

Performance Improves with Practice



Neural plasticity depends upon:

- Sensory & Motor experience
- Neuromodulators

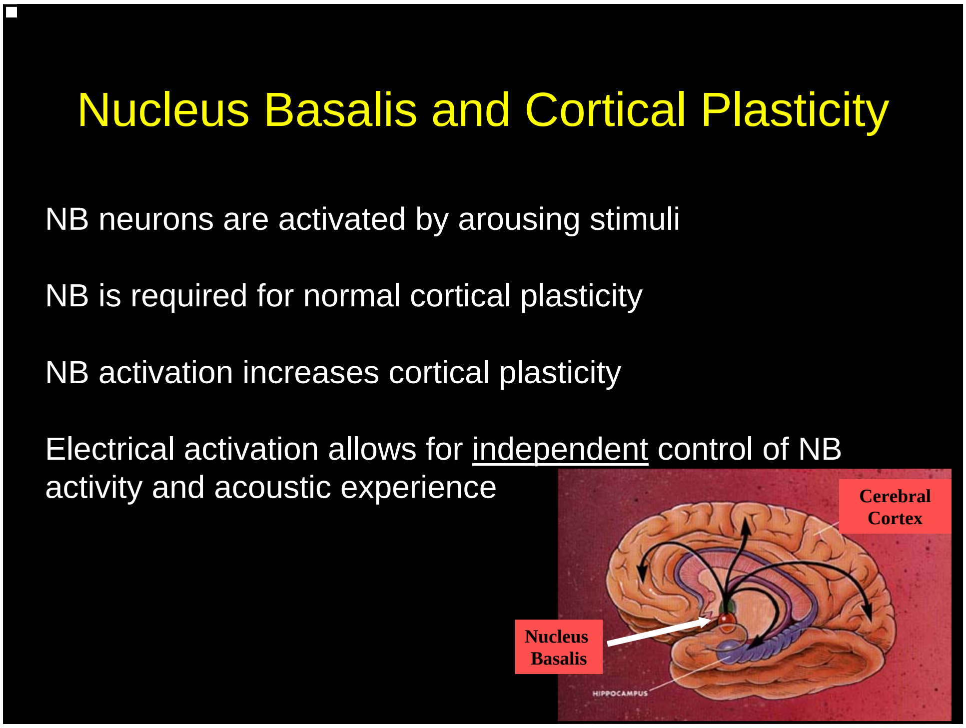


Approaches and Techniques to Induce Experience-Dependent Neuroplasticity

Behavioral Training

Nucleus Basalis Stimulation

Environmental Enrichment



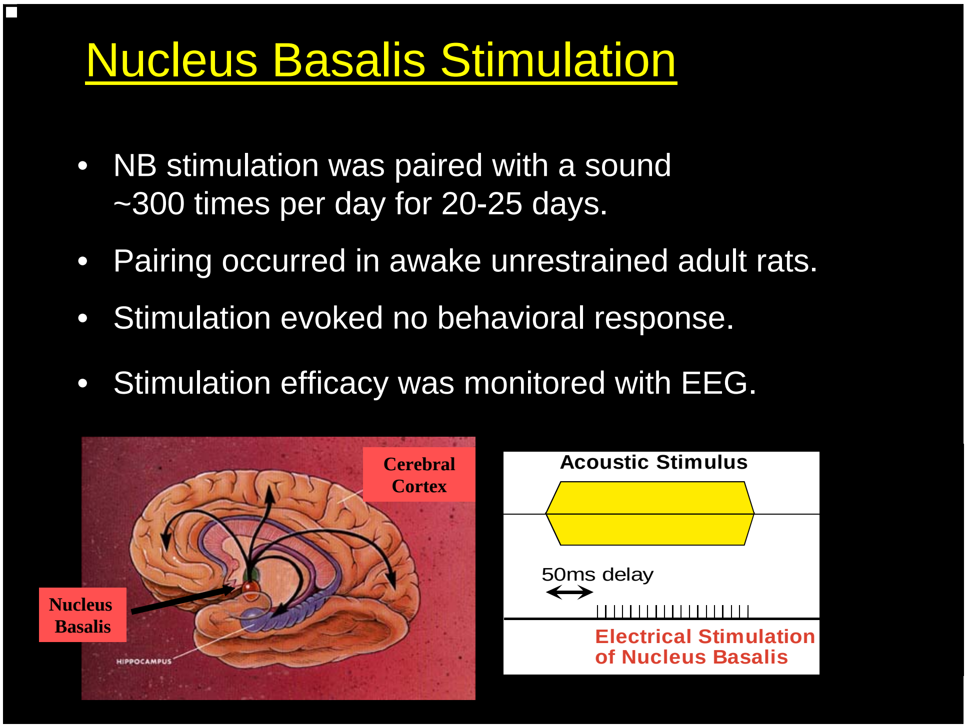
Nucleus Basalis and Cortical Plasticity

NB neurons are activated by arousing stimuli

NB is required for normal cortical plasticity

NB activation increases cortical plasticity

Electrical activation allows for <u>independent</u> control of NB activity and acoustic experience

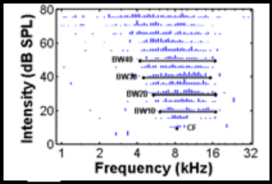


Nucleus Basalis Stimulation

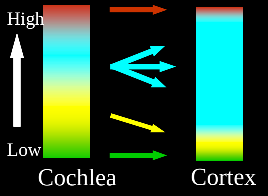
- NB stimulation was paired with a sound ~300 times per day for 20-25 days.
- Pairing occurred in awake unrestrained adult rats.
- Stimulation evoked no behavioral response.
- Stimulation efficacy was monitored with EEG.

Sensory Experience Controls:

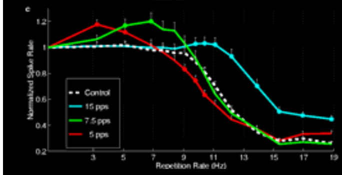
Receptive Field Size



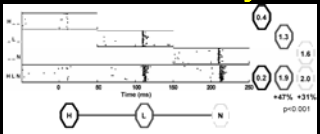
Cortical Maps

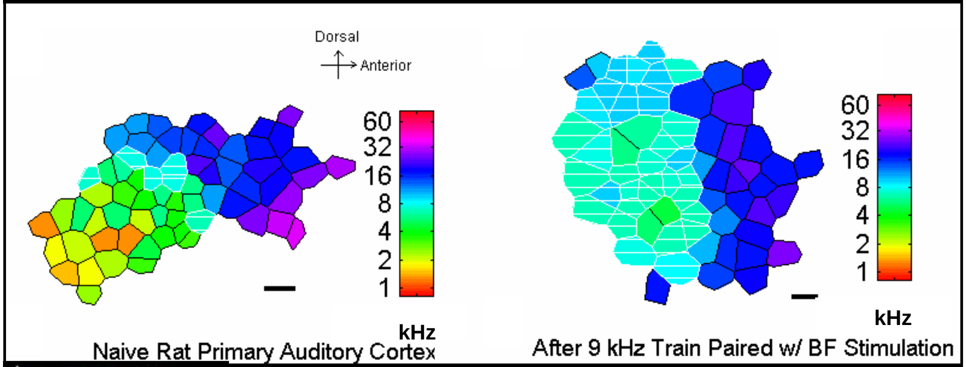


Maximum Cortical Following Rate



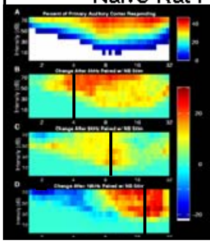
Spectrotemporal Selectivity





Naive Rat Primary Auditory Cortex

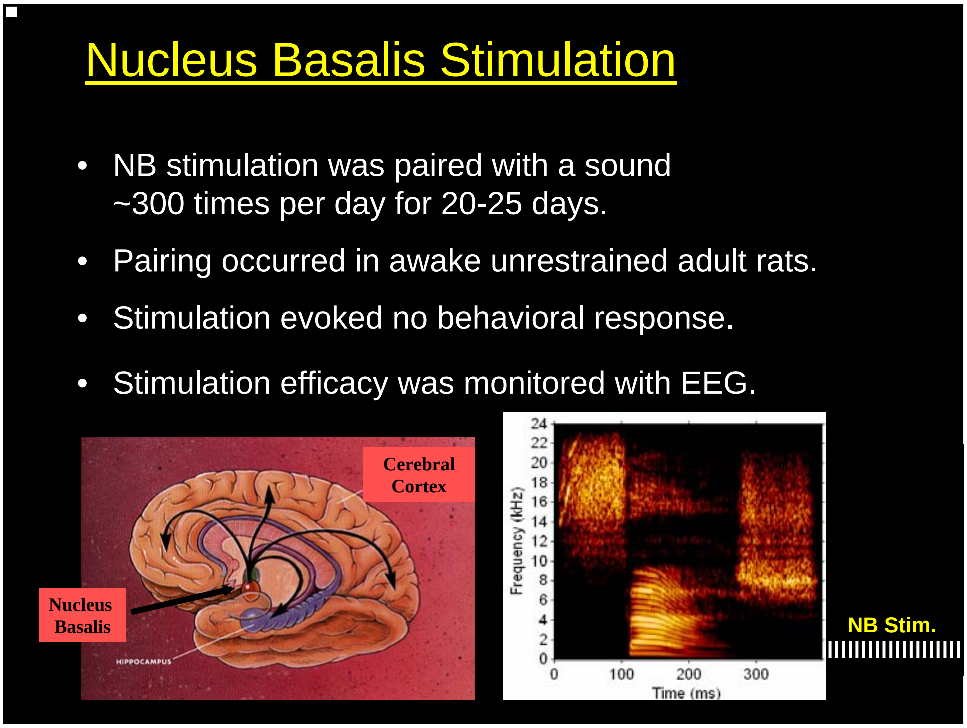
After 9 kHz Train Paired w/ BF Stimulation



Map Plasticity is Specific to the Paired Tone

Adapted from Kilgard and Merzenich Science, 1998

How does experience with speech change cortical organization?



Nucleus Basalis Stimulation

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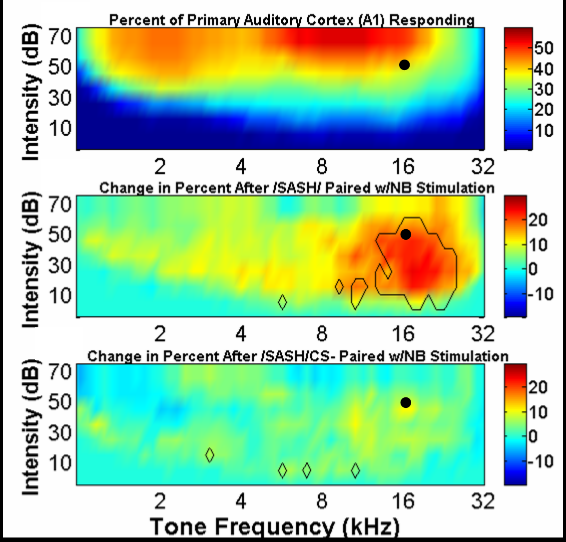
Summary of Frequency Map Plasticity



16kHz @50dB:
34 % ± 2

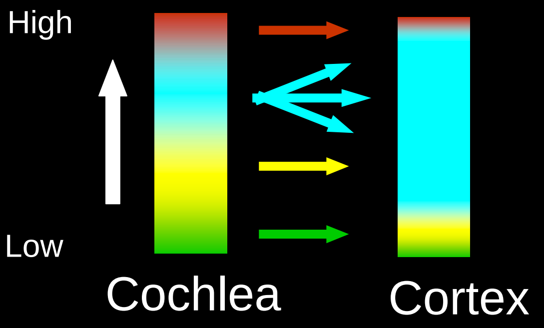
55 % ± 4.4%
P<0.0005 vs controls
~60% more neurons

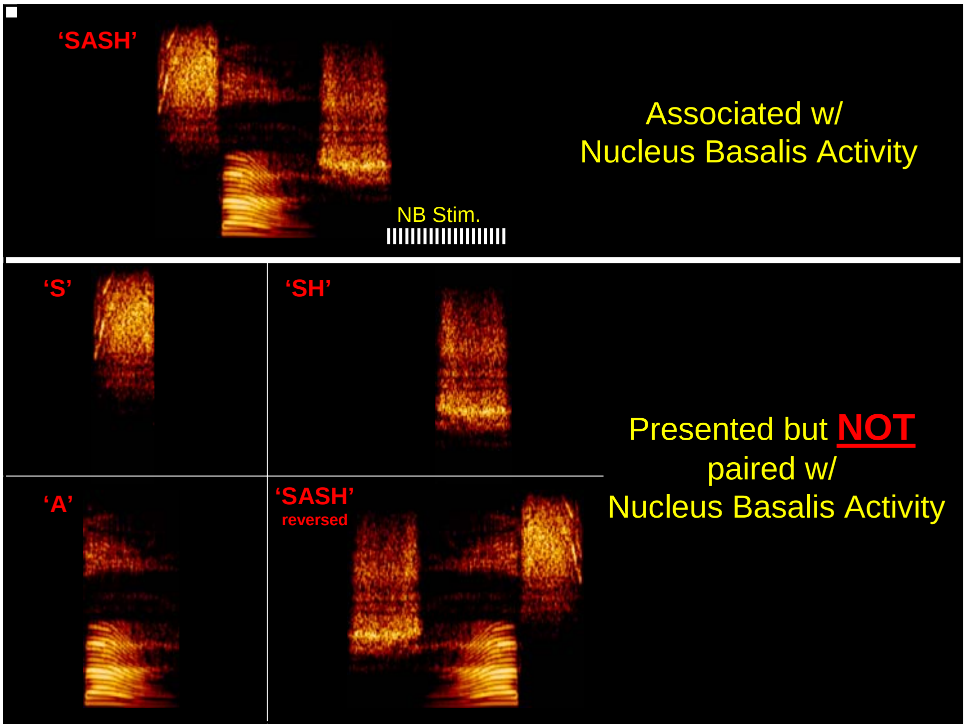
Map Plasticity **BLOCKED**

N=23, 1065 A1 sites

Pandya et al, in review

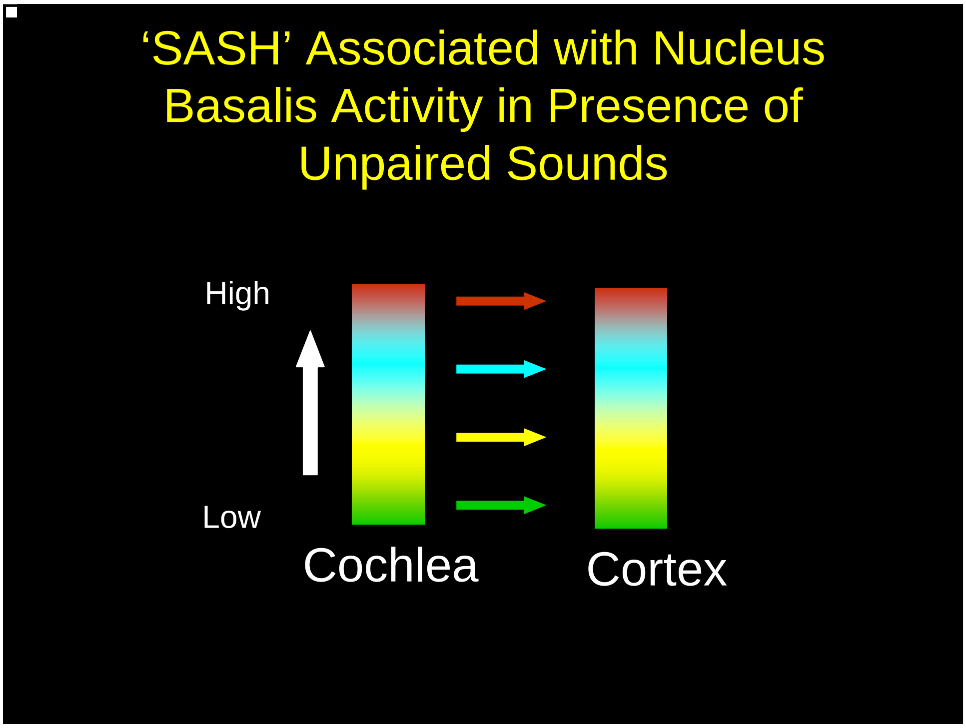
‘SASH’ Associated with Nucleus Basalis Activity





Associated w/
Nucleus Basalis Activity

Presented but **NOT**
paired w/
Nucleus Basalis Activity



'SASH' Associated with Nucleus Basalis Activity in Presence of Unpaired Sounds

Does map expansion influence masking patterns?

[YES]

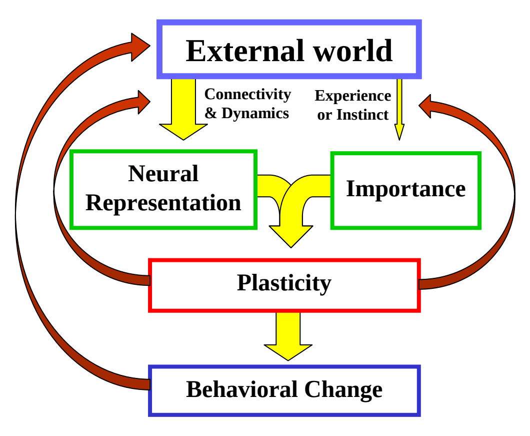
TAKE HOME MESSAGES - Neural Coding

- Neural activity patterns are determined by the spectrotemporal acoustic input
- Temporal acoustic context plays an important role in the cortical processing of natural sound patterns
- Posterior Auditory Field (PAF) is functionally distinct from Primary Auditory Cortex (A1)

TAKE HOME MESSAGES
- Neural Plasticity

- Deep brain stimulation associated w/ sound can generate large-scale reorganization of neural networks
- Cortical maps can expand, but it may not be the exclusive strategy for improving stimulus representations
- Background sounds and acoustic context exhibit a powerful influence on the expression of cortical plasticity

Exploring the Principles of Cortical Plasticity



External world

Connectivity & Dynamics

Experience or Instinct

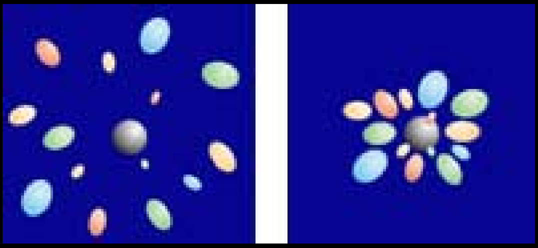
Neural Representation

Importance

Plasticity

Behavioral Change

Perceptual Magnet Effect



“Mapping” alters perception

“Reality is twisted and shaped by experience”

- Patricia Kuhl

QUESTIONS??