HST.725 Music Perception and Cognition, Spring 2009 Harvard-MIT Division of Health Sciences and Technology Course Director: Dr. Peter Cariani



Neural representation of musical pitch



Figure by MIT OpenCourseWare.

www.cariani.com

Pitch: the basis of musical tonality

- Operational definition of pitch
- Pitch of pure tones
- Pitch of harmonic complexes at the fundamental
- Pitch of the missing fundamental
- Pitch of unresolved harmonics
- Repetition pitch
- Pitch salience
- Relative vs. absolute pitch
- Pitch circularity
- Pitch: how many dimensions do we need?
- Models of pitch: Place vs. temporal theories
- Envelope vs. fine structure (Schouten & de Boer)
 - Residue theories (incomplete filtering of unresolved harmonics)
 - Temporal autocorrelation theories (Licklider)
 - Analytical (Helmholtz) vs. Gestalt (Stumpf) perspectives
 - Spectral pattern analysis/completion vs. dominant periodicity

Dimensions of auditory objects

Auditory qualities and their organization

Objects: Quasi-stationary assemblages of qualities



Dimensions of event perception

Unitary events & their organization

Events: abrupt perceptual discontinuities

TEMPORAL EVENT STRUCTURE

Timing & order (metric, sequence)

FUSION/SEPARATION

Common onset & harmonic structure => fusion Different F0s, locations, onset => separation POLYPHONY Common onset, offset => fusion Diff. meters, pitch, timbre => separation STREAMS, POLYRHYTHMS

FUSION/SEPARATION

A few words about Loudness

- Loudness is the perceptual attribute that covaries with the intensity of sounds (loudness is the subjective attribute, intensity is the physical, acoustical property)
- We mentioned that the auditory system has a huge dynamic range, over a factor of 100,000 between the sound pressure level of the softest and the loudest sounds.
- Loudness is important in music for several reasons
 - Listening level (louder music is more salient, captures attention)
 - Onsets and accents (loudness contrast accents notes)
 - **Dynamics** (changes in loudness communicate tension, relaxation)
 - Safety issues (listening to music at high levels (>100 dB SPL) for prolonged periods of time will damage your ears and impair your ability to hear music

Typical sound levels in music

Pain > 130 dB SPL

- Loud rock concert 120 dB SPL
- Loud disco 110 dB SPL
- *fff* 100 dB SPL
- f (forte, strong) 80 dB SPL
- *p* (*piano, soft*) 60 dB SPL
- *ppp* 40 dB SPL
- Lower limit
- Theshold of hearing 0 dB SPL

article.

On origins of music dynamics notation

Tuesday, February 10, 2009

Typical sound pressure levels in everyday life

The Decibel Scale Some typical sound levels



Courtsey of WorkSafe, Department of Consumer and Employment Protection, Western Australia (http://www.safetyline.wa.gov.au). http://www.safetyline.wa.gov.au/institute/level2/course18/lecture54/154_03.asp

Sound level meters and frequency weightings

- A: based on human equal loudness contours @ ~40 dB SL Fletcher-Munson curves (recently revised)
- C: flat-weighting



Graph by MIT OpenCourseWare. SPL meter photo courtesy of EpicFireworks on Flickr.

Dynamic range of some musical instruments

Images removed due to copyright restrictions.

Graphs of relative intensity vs. pitch for different instruments: violin, double bass, flute, B-flat clarinet, trumpet, french horn.Figure 8.5 in Pierce, J. R. *The Science of Musical Sound*. Revised ed. New York, NY: W.H. Freeman & Co., 1992. ISBN: 9780716760054.

Noise floor: ~ 45 dB SPL Conversation: 60 dB SPL Symphony: 80-90 dB SPL Disco: 100 dB SPL

Hearing loss with age (overexposure to loud sounds accelerates this process)



Figure by MIT OpenCourseWare.

Steps to prevent hearing damage

Use earplugs (reduce levels by 20-30 dB)



Photo courtesy of KarenD on Flickr.

Take measures in recurring situations where you experience ringing in your ears (concerts, discos) Impulsive loud sounds are worst (gunshots, hammering)

Be wary of cranking up the level in cars, especially when the windows are down (if it sounds terribly loud when you're stopped at a light, this should tell you something)

With personal sound players (MP3s, iPods, walkman), always set the listening level in quiet don't crank up the level in noisy situations use the volume limiter feature (set this in quiet) if you listen in noisy situations (mowing the lawn), then by all means use noise-cancellation headphones

Pitch in music

- Tonal music is based in large part on pitch relations
- Sequences of pitches constitute melodies
- Relations between combinations of pitches constitute harmonies
- Sets of pitches make up musical scales, which are the perceptual atoms of musical tonality
- Musical pitch is relative pitch (transpositional invariance)
- We will discuss absolute pitch later in the course

Operational definition of "pitch"

- Pitch is that auditory quality that varies with the periodicity and/or frequency of sounds.
- (i.e. not loudness, duration, location, or timbre)
- Operationally, pitch is defined as the frequency of a pure tone to which a sound is matched.
- Since pure tone pitch changes very slightly (0-4%) with large changes in sound pressure level (40 dB), the level of the reference tone also has to be specified.
- For musical sounds (complex tones), this much celebrated dependence of pitch on level is quite minimal (< 1% over 40 dB). The more harmonics, the smaller the effect.

Schematic Diagram Representing Eight Signals with the Same Low Pitch

Pitch metamery (perceptual equivalence)

Sounds with different frequency spectra can produce the same pitch



Figure by MIT OpenCourseWare.

Range of pitches of pure & complex tones

- Pure tone pitches
 - Range of hearing (30-20,000 Hz)
 - Range in tonal music (100-4000 Hz)
 - Pitches of individual partials in a complex, "analytical" pitch
- Most (tonal) musical instruments produce harmonic complexes that evoke pitches at their fundamentals (F0's)
 - Called virtual pitch, periodicity pitch, low pitch
 - Range of F0's in tonal music (30-4000 Hz)
 - Range of missing fundamental (30-1200 Hz)

Pitch is not simply frequency

Music pitches are not pure tones --They are mostly harmonic complex tones

The pitch that is heard for a harmonic complex tone corresponds to the fundamental frequency of the tone (with very few exceptions)

"Virtual" pitch: F0-pitch as pattern completion



Figure by MIT OpenCourseWare.

Figure 1. Visual analogy of virtual pitch. The visual system perceives contours which are not physically present (Terhardt, 1974).

"Missing fundamental" analogy to illusory contour

Fundamentals and harmonics

- Periodic sounds (30-20kHz) produce pitch sensations.
- Periodic sounds consist of repeating time patterns.
- The fundamental period (F0) is the duration of the repeated pattern.
- The fundamental frequency is the repetition frequency of the pattern.
- In the Fourier domain, the frequency components of a periodic sound are all members of a harmonic series (n = 1*F0, 2*F0, 3*F0...).
- The fundamental frequency is therefore the greatest common divisor of all of the component frequencies.
- The fundamental is also therefore a subharmonic of all component frequencies.





- A. Fundamental sine wave.
- B. Fundamental, second harmonic, and the resultant.
- C. Fundamental, second and third harmonics, and the resultant.
- D. Fundamental, second, third, and fourth harmonics, and the resultant.
- E. Fundamental, second, third, fourth, and fifth harmonics, and the resultant.

Emergent pitch



Autocorrelation (positive part)



Harmonic series

A harmonic series conists of integer multiples of a fundamental frequency, e.g. if the fundamental is 100 Hz, then the harmonic series is: 100, 200, 300, 400, 500, 600 Hz, etc.

The 100 Hz fundamental is the *first harmonic*, 200 Hz is the *second* harmonic. The fundamental is often denoted by F0.

The fundamental frequency is therefore the greatest common divisor of all the frequencies of the partials.

Harmonics above the fundamental constitute the overtone series.

Subharmonics are integer divisions of the fundamental: e.g. for F0= 100 Hz, subharmonics are at 50, 33, 25, 20, 16.6 Hz etc. Subharmonics are also called *undertones*.

The fundamental period is 1/F0, e.g. for F0=100 Hz, it is 1/100 sec or 10

Auditory system: Frequency analyzer vs. Periodicity analyzer

Conceptual models of resonance:

Helmholz resonator band-pass filter -- one frequency frequency decomposition simple oscillator models

String many harmonics comb filter

Figure by MIT OpenCourseWare.

Complex oscillator - delay loop matched filter, complex pattern generator





Figure by MIT OpenCourseWare.

Helmholtz resonator

http://www.phys.unsw.edu.au/jw/Helmholtz.html



Sirens



A simple siren is produced by forcing compressed air through equally spaced holes on a rotating disk. This produces a periodic vibration whose frequency equals the rate of holes passing by the air nozzle.



De la Tour's siren

Early sound analysis of vowels



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In this 19th century apparatus developed by Koenig, waveforms were visualized by viewing a flame reflected on a rotating mirrored drum. Vowel sounds resulted in the same flame pattern regardless of their pitch level.



Pitch - best fitting template

Correlograms

Images removed due to copyright restrictions.

See Figures 6.16A-D and 6.17 in Lyon, R. and S. Shamma. "Auditory Representations of Timbre and Pitch." In *Auditory Computation*. Edited by R. R. Fay. New York, NY: Springer, 1996.

Licklider virtual pitch masking demonstration (iTunes/Spectrograph)





Wednesday, February 11, 2009



Many different sounds produce the same pitches

Strong

- Pure tones
- Harmonic complexes
- Iterated noise

Weaker

- High harmonics
- Narrowband noise

Very weak

- AM noise
- Repeated noise

Weaker low pitches

Strong

pitches





Figure by MIT OpenCourseWare.

As harmonic numbers increase, the missing fundamental gets weaker.



- Highly precise percepts
 - Musical half step: 6% change F0
 - Minimum JND's: 0.2% at 1 kHz (20 usec time difference, comparable to ITD jnd)

Pitch basics

- Highly robust percepts
 - Robust quality Salience is maintained at high stimulus intensities
 - Level invariant (pitch shifts < few % over 40 dB range)
 - Phase invariant (largely independent of phase spectrum, f < 2 kHz)

Strong perceptual equivalence classes

- Octave similarities are universally shared
- Musical tonality (octaves, intervals, melodies) 30 Hz 4 kHz
- Perceptual organization ("scene analysis")
 - **Fusion:** Common F0 is a powerful factor for grouping of frequency components
- Two mechanisms? Temporal (interval-based) & place (rate-based)
 - **Temporal:** predominates for periodicities < 4 kH (level-independent, tonal)
 - Place: predominates for frequencies > 4 kHz(level-dependent, atonal)

Pure tone pitch discrimination becomes markedly worse above 2 kHz

Weber fractions for frequency (Δf/f) increase 1-2 orders of magnitude between 2 kHz and 10 kHz



Figure by MIT OpenCourseWare.

JND's



Figure by MIT OpenCourseWare.

Pure tone pitch discrimination improves

at longer tone durations

and

at higher sound pressure levels



Figure by MIT OpenCourseWare.

"Pitchedness" as a function of sound duration

Graph removed due to copyright restrictions.

Figure 36, comparing "Tone pitch" and "click pitch" response. In Licklider, J. C. R. "Basic Correlates of the Auditory Stimulus." *Handbook of experimental psychology*. Edited by S. S. Stevens. Oxford, UK: Wiley, 1951. pp. 985-1039.



The neural coding problem in audition:

How does the brain represent and process acoustic patterns, such that we hear what we hear?

In particular, how does it represent periodic sounds, such that we hear pitches at the fundamentals of musical sounds?



Figure by MIT OpenCourseWare.




Figure by MIT OpenCourseWare.

Ear and cochlea





Neural frequency tuning PLACE PRINCIPLE

Disconnect between cochlear tuning & pitch discrimination for freqs < 4 khz

CF = characteristic frequency



Figure by MIT OpenCourseWare.

Temporal coding in the auditory nerve

Cat, 100x @ 60 dB SPL





Reprinted with permission, from Secker-Walker HE, Searle CL. 1990. "Time-domain Analysis of Auditory-nerve-fiber Firing Rates." J Acoust Soc Am 88 (3): 1427-36. Copyright 1990, Acoustical Society of America.

Phase-locking in auditory nerve fibers

250 Hz tone



Figure by MIT OpenCourseWare.

See Javel E, McGee JA, Horst W, Farley GR, "Temporal mechanisms in auditory stimulus coding." In: G. M. Edelman, W. E. Gall and W. M. Cowan, ed, Auditory Function: Neurobiological Bases of Hearing, Wiley: New York 1988; p. 518.

Auditory nerve fiber responses to a periodic sound



Interspike intervals in the auditory nerve encode stimulus periodicities



Figure by MIT OpenCourseWare.

Global temporal pitch representation (Collaborator B. Delgutte)

•<u>All-order</u> interspike intervals •Population-wide distribution: –<u>All</u> auditory nerve fibers –(all CFs, all SRs)

Predictions

<u>Pitch (frequency)</u> = the predominant interval or interval pattern
<u>Pitch strength (salience)</u> = the relative fraction of pitch-related intervals in the whole distribution
<u>Detectability:</u> A pitch can be heard iff its salience





290



All-order interval histograms

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Source: Cariani, P. A., and B. Delgutte. "Neural Correlates of the Pitch of Complex Tones. I. Pitch and Pitch Salience." J Neurophysiol 76 (1996): 1698-1716. [0022-3077/96].

Construction of the population-interval

distribution

of the auditory nerve

(Cariani & Delgutte, J. Neurophysiol. 1996)

Courtesy of the American Physiological Association. Used with permission.

spikes # 250 260 270 280

Peristimulus time (ms)

240

Population-interval histogram



Stimulus Autocorrelation



All-order interval histograms





Autocorrelation functions



Source: Cariani, P. A., and B. Delgutte. "Neural Correlates of the Pitch of Complex Tones. I. Pitch and Pitch Salience." *J Neurophysiol* 76 (1996): 1698-1716. [0022-3077/96]. Courtesy of the American Physiological Association. Used with permission.

Many different sounds produce the same pitches

Strong pitches

Strong

- Pure tones
- Harmonic complexes
- Iterated noise

Weaker

- High harmonics
- Narrowband noise

Very weak

- AM noise
- Repeated noise

Weaker low pitches

Schematic Diagram Representing Eight Signals with the Same Low Pitch



Figure by MIT OpenCourseWare.

125 Hz

250 Hz 50

500 Hz

Many different sounds produce the same pitch pitch metamery

Fastl, H. & Stoll, G. Scaling of pitch strength, Hearing Research 1(1979): 293-301



Wednesday, February 11, 2009

Courtesy Elsevier, Inc., http://www.sciencedirect.com. Used with permission.

Use the structure of perception to find neural codes:

- 1. Use stimuli that produce equivalent percepts
- 2. Look for commonalities in neural response
- 3. Eliminate those aspects that are not invariant



Pitch equivalence classes

(keep the percept constant, identify neural response invariances)





van Norden, 1981; after Ritsma (1962)

Level-invariance

Pitch equivalence



Figure by MIT OpenCourseWare.

A correlational representation for loudness?



Correlation between population-interval distributions and stimulus autocorrelation serves as an index of the amount of common, stimulus-driven time structure in the auditory nerve array.

> As the sound pressure level increases, a progressively greater fraction of the activity in the array is stimulus locked and mutually correlated.

> This representation makes use of the dynamic range of the entire auditory nerve array, and leads to a theory of partial loudnesses of multiple auditory objects in a very straightforward way.

Wednesday, February 11, 2009



Population-interval distributions and autocorrelation functions

> Pure Tone 160 Hz

AM Tone Fm =160 Hz Fc = 640 Hz

Click Train F0 = 160 Hz

AM Broadband Noise Fm = 160 Hz



The running population-interval distribution



Population interval histograms (cross sections)



Pitch shift of inharmonic complex tones





Peristimulus time (ms)

Pitch shift of inharmonic complex tones Phase-invariant nature of all-order interval code

AM Tone QFM Tone Fc=640 Hz, Fm=200 Hz Fc=640 Hz, Fm=200 Hz MMMMMMMв 80 100 100 1 kHz 1 kHz Peristimulus time (ms) Freq Peristimulus time (ms) Freq Fc=640 Hz, Fm=160-320 Hz D F_c=640 Hz, F_m=160-320 Hz 15 15 Interval (ms) 10 10 de Boer's rule 1/Fm 100 200 300 500 100 200 300 400 500 400 0 Peristimulus time (ms) Peristimulus time (ms)

AM Tone





Wednesday, February 11, 2009

Cochlear nucleus IV: Pitch shift



Wednesday, February 11, 2009

Dominance region for pitch (harmonics 3-5 or partials 500-1500 Hz)





Harmonics 3-5 and 6-12 presented separately

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Coding of vowel quality (timbre)



Pitch masking

What degree of temporal correlation is necessary for pitch to become audible?

١

Variable-F0 click train in broad-band noise Click train: F0= 160-320 Hz, positive polarity, 80 dB SPL Peak/background ratio: intervals @ $1/F0 \pm 150$ usec/mean over all intervals Informal pitch thresholds, s/n dB: 12 (MT), 13 (PC), 16 (BD)

Below threshold (no pitch)

s/n: 8 dB p/b = 1.11



Above threshold (weak pitch)

p/b = 1.57

300

s/n: 20 dB

Above threshold (strong pitch)

s/n: 32 dB p/b = 2.38



Above threshold (strong pitch)



Peristimulus time (ms)

Vowels

Population-interval coding of timbre (vowel formant structure)



Population-wide distributions of short intervals for 4 vowels





Reprinted with permission, from Secker-Walker HE, Searle CL. 1990. "Time-domain Analysis of Auditory-nerve-fiber Firing Rates." *J Acoust Soc Am* 88 (3): 1427-36. Copyright 1990, Acoustical Society of America.

Summary

Population-interval representation of pitch at the level of the auditory nerve



Temporal coding of pitch in the auditory nerve

Pitch = predominant all-order interspike interval

Pitch strength = relative proportion of pitch-related intervals

Timbre (tone quality) = pattern of other intervals

Stimulus autocorrelation ~ population-interval distribution

Readily explains:

- Pitch equivalence classes
- Invariance w. Δ sound pressure level
- Invariance w. Δ waveform envelope, phase spectrum
- Existence region of musical tonality (octaves, melody)
- Pitches of resolved & unresolved harmonics
- Pitches of harmonic & inharmonic tone complexes




Wednesday, February 11, 2009 (2001): 107-135. DOI: 10.1076/jnmr.30.2.107.7115. This journal is available online at http://www.ingentaconnect.com/content/routledg/jnmr/

Correlations between population-interval patternsPure tonesHarmonics 1-6



This image is from the article Cariani, P. "Temporal Codes, Timing Nets, and Music Perception." *Journal of New Music Research* 30, no. 2 (2001): 107-135. DOI: 10.1076/jnmr.30.2.107.7115. This journal is available online at http://www.ingentaconnect.com/content/routledg/jnmr/

Existence region of musical tonality is coextensive with spike timing information

Musical tonality: octaves, intervals, melodies

Strong phase-locking (temporal information)

Phase-locking as measured by synchronization index declines dramatically above ~4 kHz





10k



30 100 1k Frequency (kHz)

Duplex time-place representations



Two codes for "pitch

Place code

Pitch = place of excitation

Pitch height

Absolute

Low vs. high

Existence region f: .100-20,000 Hz

Frequency analysis Fourier spectrum

Time code

Pitch = dominant periodicity

Musical pitch "Chroma", Tonality

Relational

Musical intervals, tonality Melodic recognition & transposition

Existence region F0: 30-4000 Hz

> Periodicity analysis Autocorrelation

Pitch dimensions: height & chroma



a Shepard scale that goes around in circle.

Figure by MIT OpenCourseWare.

Pitch height and pitch chroma

Images removed due to copyright restrictions.

Figures 1, 2, and 7 in Shepard, R. N. "Geometrical Approximations to the Structure of Musical Pitch." *Psychological Review* 89, no. 4 (1982): 305-322.

Temporal theories - pros & cons

Make use of spike-timing properties of elements in early processing (to midbrain at least) Interval-information is precise & robust & levelinsensitive

No strong neurally-grounded theory of how this information is used

 Unified model: account for pitches of perceptuallyresolved & unresolved harmonics in an elegant way (dominant periodicity)
 Explain well existence region for F0 (albeit with limits on max interval durations)
 Do explain low pitches of unresolved harmonics

Interval analyzers require precise delays & short coincidence windows

Spectral pattern models

Mostly conceived within a frequency analysis framework

"Auditory filters" derived from psychophysics, not physiology

Shapes of perceptually-derived "auditory filters" (Moore)



Don't conflate these with cochlear filters or auditory nerve excitation patterns! Auditory filters are derived from psychophysical data & reflect the response of the whole auditory system. For lower frequencies and higher levels AFs have much narrower bandwidths than cochlear resonances or auditory nerve fiber responses.



Wednesday, February 11, 2009

From masking patterns to "auditory filters" as a model of hearing

Power spectrum Filter metaphor

Notion of one central spectrum that subserves



2.2. Excitation pattern Using the filter shapes and bandwidths derived from masking experiments we can produce the excitation pattern produced by a sound. The excitation pattern shows how much energy comes through each filter in a bank of auditory filters. It is analogous to the pattern of vibration on the basilar membrane. For a 1000 Hz pure tone the excitation pattern for a normal and for a SNHL (sensori-neural hearing loss) listener look like this: The excitation pattern to a complex tone is simply the sum of the patterns to the sine waves that make up the complex tone (since the model is a linear one). We can hear out a tone at a particular frequency in a mixture if there is a clear peak in the excitation pattern at that frequency. Since people suffering from SNHL have broader auditory filters their excitation patterns do not have such clear peaks. Sounds mask each other more, and so they have difficulty hearing sounds (such as speech) in noise. --Chris Darwin, U. Sussex, http://www.biols.susx.ac.uk/home/Chris_Darwin/Perception/Lecture_Notes/Hearing3/ hearing3.html

Courtesy of Prof. Chris Darwin (Dept. of Psychology at the University of Sussex). Used with permission.

Resolvability of harmonics (Plomp, 1976)

Fundamental frequency (F0) Image removed due to copyright restrictions. Graph of frequency separation between partials vs. frequency of the partial. From Plomp, R. *Aspects of Tone Sensation*. New York, NY: Academic Press, 1976.

Resolution of harmonics (based on psychophysics)



Figure by MIT OpenCourseWare.

Goldstein's harmonic templates

Figure removed due to copyright restrictions. Diagram of periodicity pitch as harmonic frequency pattern recognition. Figure 3 in Goldstein, J. L., et al. "Verification of the Optimal Probabilistic Basis of Aural Processing in Pitch of Complex Tones." *J Acoust Soc Am* 63 (1978): 486-510. http://dx.doi.org/10.1121/1.381749 A "two-mechanism" perspective (popular with some psychophysicists)



Julius Goldstein references

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Terhard's method of common subharmonics

Spectral vs. virtual pitch: duplex model Virtual pitch computation:

- 1. Identify frequency component
- 2. Find common subharmonics
- 3. Strongest common subharmonic after

F0 weighting is the virtual pitch

Terhardt's model has been extended by

Parncutt to cover pitch multiplicity

and fundamental bass of chords

Terhardt references

Terhardt E (1970) Frequency analysis and periodicity detection in the sensations of roughness and periodicity pitch. In: Frequency Analysis and Periodicity Detection in Hearing (Plomp R, Smoorenburg GF, eds). Leiden: A. W. Sijthoff.

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SPINET:

Cohen Grossberg, Wyse JASA

Fixed neural network: connection weights arranged so as to form pitch-equivalence classes

Courtesy of Prof. Stephen Grossberg. Used with permission. Source: Cohen, M. A., S. Grossberg, and L. L. Wyse. "A Spectral Network Model of Pitch Perception." Technical Report CAS/CNS TR-92-024, Boston University. Also published in *J Acoust Soc Am* 98, no. 2 part 1 (1995): 862-79.



Broad tuning and rate saturation at moderate levels in low-CF auditory nerve fibers confounds rate-based resolution of harmonics.

Low SR auditory nerve fiber



Spectral pattern theories - pros & cons

Do make use of frequency tuning properties of elements in the auditory system No clear neural evidence of narrow (< 1/3 octave) frequency channels in low-BF regions (< 2 kHz)

Operate on perceptually-resolved harmonics Do not explain low pitches of unresolved harmonics

Require templates or harmonic pattern analyzers Little or no neural evidence for required analyzers Problems w. templates: relative nature of pitch

Do not explain well existence region for F0 Learning theories don't account for F0 ranges or for phylogenetic ubiquity of periodicity pitch

Problems with rate-place models

In contrast to musical (F0) pitch percepts....

Rate-place spectral profiles

- have coarse resolution (\geq 1 octave)
- change with sound level
- worsen dramatically at higher sound levels
- should work better for high frequencies
- cannot account for F0 pitches of unresolved harmonics





Modulation detectors in the midbrain

Stimulus-related temporal discharge patterns

Modulation-tuning of discharge rate

Images removed due to copyright restrictions.

See Fig. 2 and 3 in Langner, G. and C. E. Schreiner.

"Periodicity Coding in the Inferior Colliculus of the Cat. I. Neuronal Mechanisms."

J Neurophysiol 60 (1988): 1799-1822.

See: Günter Ehret (1997) The auditory midbrain, a "shunting yard" of acoustical information processing.
In *The Central Auditory System*, Ehret, G. & Romand, R., eds. Oxford University Press.
Langner, G. and Schreiner, C.E. Periodicity coding in the inferior colliculus of the cat. I. Neuronal mechanisms. *J. Neurophysiol.* 60:1799-1822.
Langner (1992) review, Periodicity coding in the auditory system. *Hearing Research*, 60:115-142.

Pitch-related temporal patterns in field potentials in awake monkey cortex

Figure. Averaged cor tical field potentials (current source densi ty analysis, lower lamina 3, site BF=5 kHz) in response to 50 ms click trains F0=100-500 Hz. Ripples up to 300-400 Hz show synchronized component of the ensembleresponse, From Steinschneider (1999).

Image removed due to copyright restrictions. See Fig. 9 right, in Steinschneider, M., et al. "Click Train Encoding in Primary Auditory Cortex of the Awake Monkey: Evidence for Two Mechanisms Subserving Pitch Perception." *J Acoust Soc Am* 104, no. 5 (1998): 2935-2955. DOI: 10.1121/1.423877.



Courtesy of Prof. Mark J. Tramo, M.D., Ph.D. Used with permission.

Source: Tramo, Mark J. "Neural Representations of Acoustic Information in Relation to Voice Perception." Havard University PhD Thesis, 1999.

Pure tone temporal response profiles in auditory cortex (A1)



Courtesy of Prof. Mark J. Tramo, M.D., Ph.D. Used with permission.

Source: Tramo, Mark J. "Neural Representations of Acoustic Information in Relation to Voice Perception." Havard University PhD Thesis, 1999.

Phase-locking in thalamus and cortex

De Ribaupierre: 10% of thalamic units in awake cats with synchronization indices of 0.3 or better to 1-2 kHz tones

Reports of isolated cortical units with phase-locking to Fm of AM tones up to 1 kHz (Semple)

Pitch detectors in thalamus and cortex

Schwarz & Tomlinson failed to find true F0 detectors in their study of > 200 cortical units in awake macaque

Riquimaroux found 16 units that responded both to pure tones and harmonic complexes that would evoke the same pitch

Bendor & Wang(2005) F0-tuned units in auditory cortex

Image removed due to copyright restrictions. See Fig. 1 in Bendor and Wang. "The Neuronal Representation of Pitch in Primate Auditory Cortex." *Nature* 436 (2005): 1161-1165. The tight correspondences between psychophysics and the population interspike interval code **strongly** suggest that our perception of pitch depends on this information.

Yet, despite some recent advances, we still do not understand how the central auditory system uses this information.

What happens to neural timing information as one ascends the auditory pathway from auditory nerve to cortex?

Is time converted to some sort of place code (e.g. pitch detectors) or is some other kind of code involved?

Discharge rate as a function of frequency and intensity

Auditory nerve fiber

Rose (1971)



Figure by MIT OpenCourseWare.

Four graphs removed due to copyright restrictions. See Fig. 2 and Fig. 4 in Rose, J. E., et al. "Some Effects of Stimulus Intensity on Response of Auditory Nerve Fibers in the Squirrel Monkey." *J Neurophysiol* 34 (1971): 685–699.

Frequency response curves for fibers in the cochlear nerve of the squirrel monkey. Left: low spontenous activity; right: high spontaneous activity.

From Rose, J. E., et al. "Some Effects of Stimulus Intensity on Response of Auditory Nerve Fibers in the Squirrel Monkey." J Neurophysiol 34 (1971): 685–699.

Alan Palmer In Hearing, Moore ed.

Figure 4 in Palmer, Alan. "Neural Signal Processing." Chapter 3 in *Hearing*. 2nd ed. Edited by B. C. J. Moore. Academic Press, 1995. [Preview this image in Google Books]

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