

# Neural computations in the time domain

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### Summary

**We propose simple neural timing mechanisms that:**

- 1) compare time structures of spike trains associated with two sounds to extract common pitches & timbres**
- 2) detect arbitrary recurrent time patterns in their inputs**
- 3) separate multiple auditory objects**

### **Abstract**

In the auditory nerve, there is an abundance of temporal information that precisely and robustly encodes many perceptually-relevant aspects of acoustic stimuli: periodicity, spectral shape, speech modulations, rhythms, and still longer time structures. Most central models of auditory processing that utilize this timing information have assumed that a time-to-place transformation must occur in the ascending auditory pathway, such that central representations of auditory forms are based on excitation profiles of frequency- or periodicity-tuned units. In these models, auditory discrimination and recognition is performed by comparing stored excitation profiles with incoming ones.

However, if timing information can be somehow be preserved and stored centrally, then purely temporal analyses of similarity and difference can be carried out by temporal correlation operations. Three very basic neural timing architectures that utilize coincidence detectors and tapped delay lines are proposed. A feed-forward network of tapped delay lines and coincidence detectors can compute cross-correlations and convolutions on pulse trains. Periodicities common to the input pulse trains appear in the time structure of the outputs, such that the array functions as a temporal sieve. To the extent that time structure of inputs reflect those of stimuli, such arrays can compute pitch similarity irrespective of timbre, and timbral similarity independent of pitch. If coincidence elements with local inhibitory connections are added to arrays of all-pass units, pulse coincidences are vetoed, and an anti-correlation, cancellation operation is performed.

A coincidence network with many recurrent delay paths can function as a reverberating memory. Incoming time patterns are cross-correlated with previously stored patterns circulating through each delay loop. The circulating patterns set up temporal expectations that are either reinforced or attenuated depending upon subsequent inputs (cf. Patterson & Allerhand, J. Acoust. Soc. Am. 98:1890-4). Time patterns of auditory objects with different fundamentals segregate into different reverberant loops each with its own corresponding recurrence time.

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## Population-interval representations

Population interval representations are population-wide distributions of all-order interspike intervals (i.e. intervals between both consecutive and nonconsecutive spikes in the same spike train).

Population-interval distributions at the level of the auditory nerve and cochlear nucleus constitute autocorrelation-like representations capable of subserving the perception of complex auditory forms such as pitch, timbre, and rhythm. What kinds of neural computations could effectively use such global timing information?

**Autocorrelation-like representations.** We observed empirically that patterns of major and minor peaks in population-representations resemble those of their respective stimulus autocorrelation functions. This is a general consequence of phase-locking of discharges. To the extent that a receptor system produces neural discharges whose timings are highly correlated with stimulus time structure, distributions of all-order interspike intervals will resemble the stimulus autocorrelation function. In the auditory system, population-interval distributions can provide very general, precise, and robust vehicles for encoding stimulus periodicities below 5 kHz.

**Representations of pitch.** Features of population-interval distributions estimated from responses of 50-100 single auditory nerve fibers of Dial-anesthetized cats closely parallel human pitch perception (Cariani & Delgutte, J. Neurophysiol. 76(3):1698-1734, 1996). With very few exceptions, the most frequent all-order interval in the auditory nerve at any given time corresponds to the pitch that is heard. Periodic stimuli produce population-interval distributions whose major interval peaks are associated with the fundamental period and its multiples. Ratios of pitch-related intervals to all others qualitatively correspond to pitch salience. Many pitch-related phenomena are readily explained in terms of population-interval distributions: pitch of the missing fundamental, pitch equivalence, phase & level invariances, nonspectral pitch, dominance region, and inharmonic pitch shifts.

**Representations of the timbres of stationary sounds.** The timbre of stationary harmonic sounds is associated with shapes of spectral envelopes and patterns of minor peaks in autocorrelation functions. All stimulus components contribute their time structure to population interval distributions to the degree that they produce stimulus-locked discharges. While patterns of major interval peaks in population interval distributions are associated with pitch, patterns of minor peaks are associated with timbre. In the auditory nerve, different vowels produce population-interval distributions with patterns of short intervals that are characteristic of formant structure.

# Population-interval coding of pitch

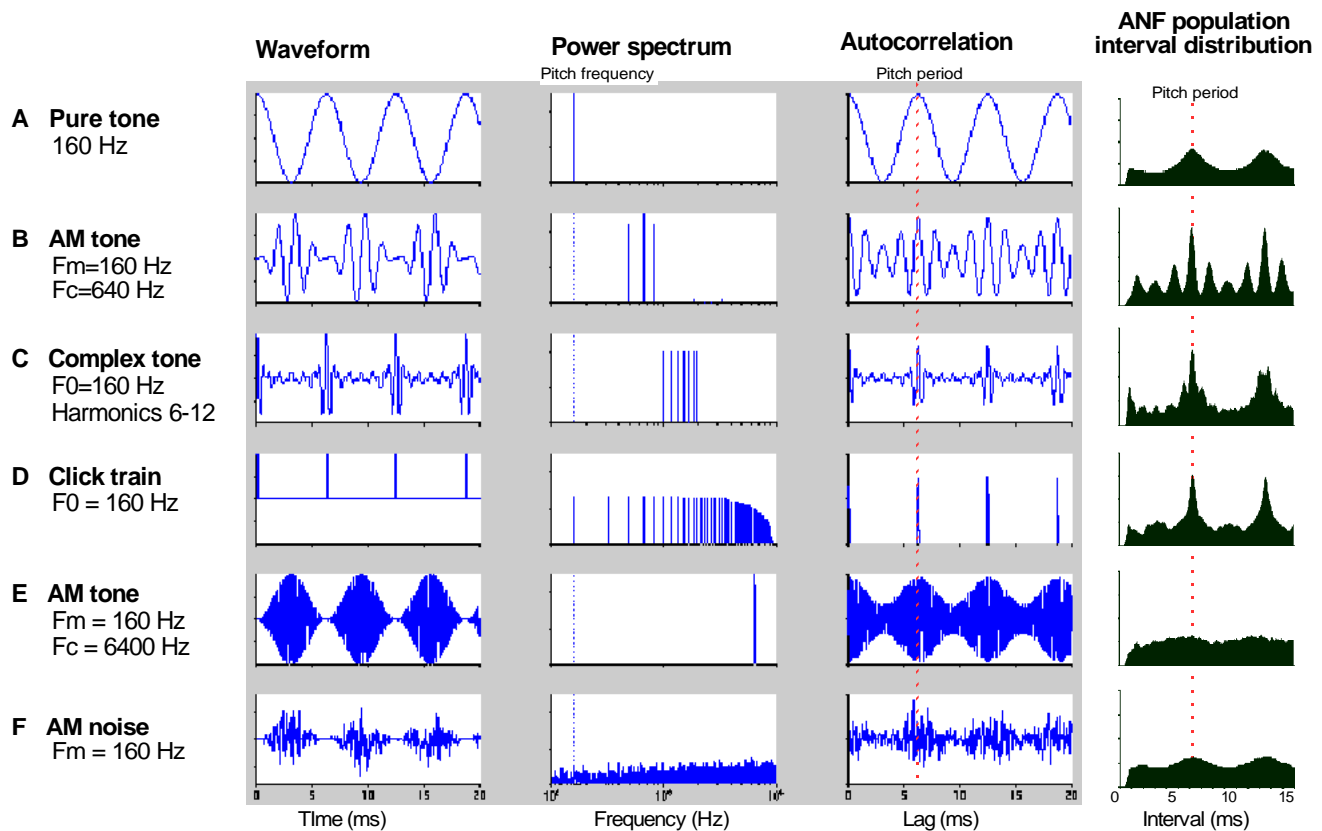


Figure 2. Stimulus waveforms, power spectra, autocorrelation functions, and population-interval distributions for 6 diverse stimuli that produce pitches at 160 Hz. The top four stimuli produce strong pitches, while the bottom two produce weak and/or indefinite pitches. Population-interval distributions were constructed from responses of 49-85 auditory nerve fibers. All stimuli presented at 60 dB total SPL. Positions of major interval peaks correspond to pitch periods. (From Cariani & Delgutte, 1996)

# Population-interval coding of timbre (vowel formant structure)

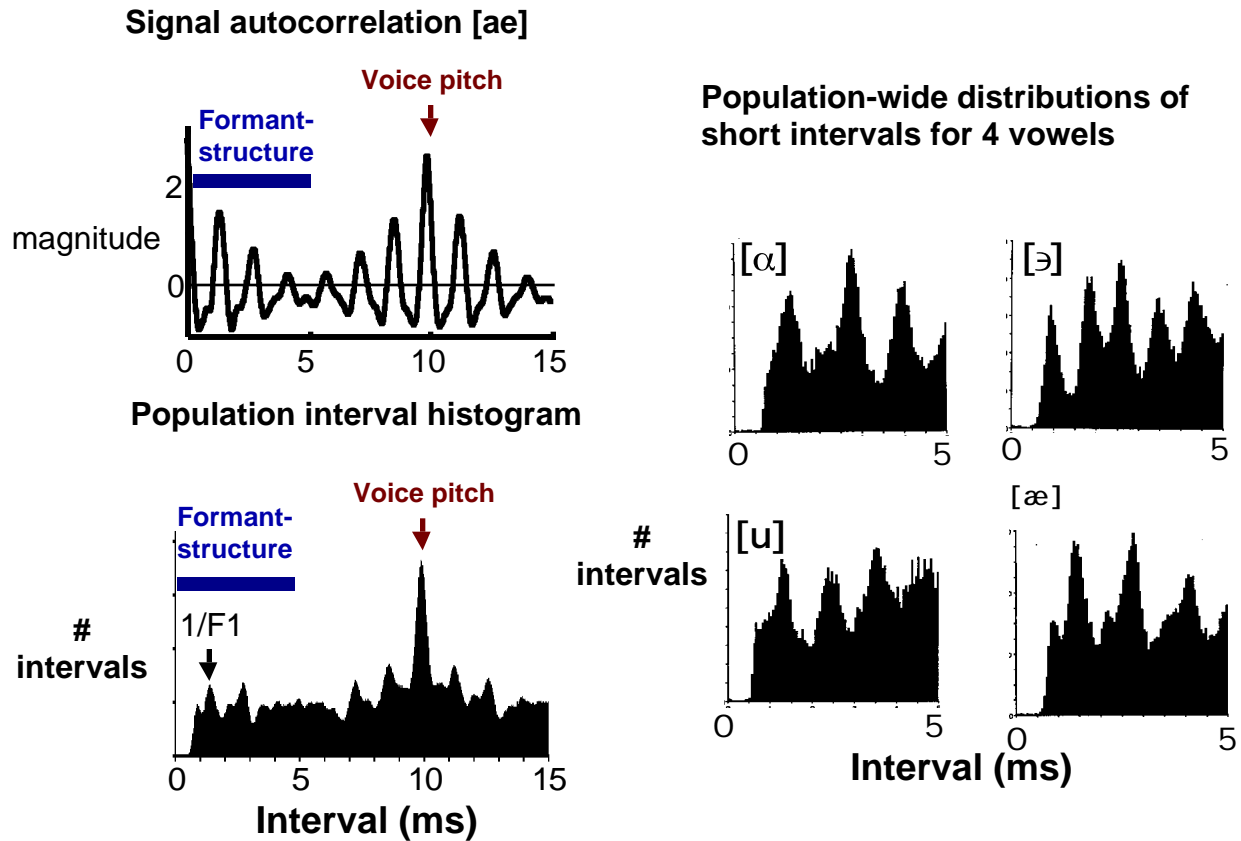


Figure 3. Left: Autocorrelation-like representations of four vowels. Left: Stimulus autocorrelation function (top) and response population interval distribution of 71 auditory nerve fibers. Stimulus: 5-formant synthetic vowel [æ] (as in "had") with formants at 750, 1450, 2450, 3350, 3850 Hz, and fundamental frequency  $F_0 = 100$  Hz., 100x, 60 dB SPL. Right: Population-wide distributions of short interspike intervals for 4 synthetic 5-formant vowels.

# Comparison of population-interval distributions with stimulus autocorrelation functions for four musical intervals

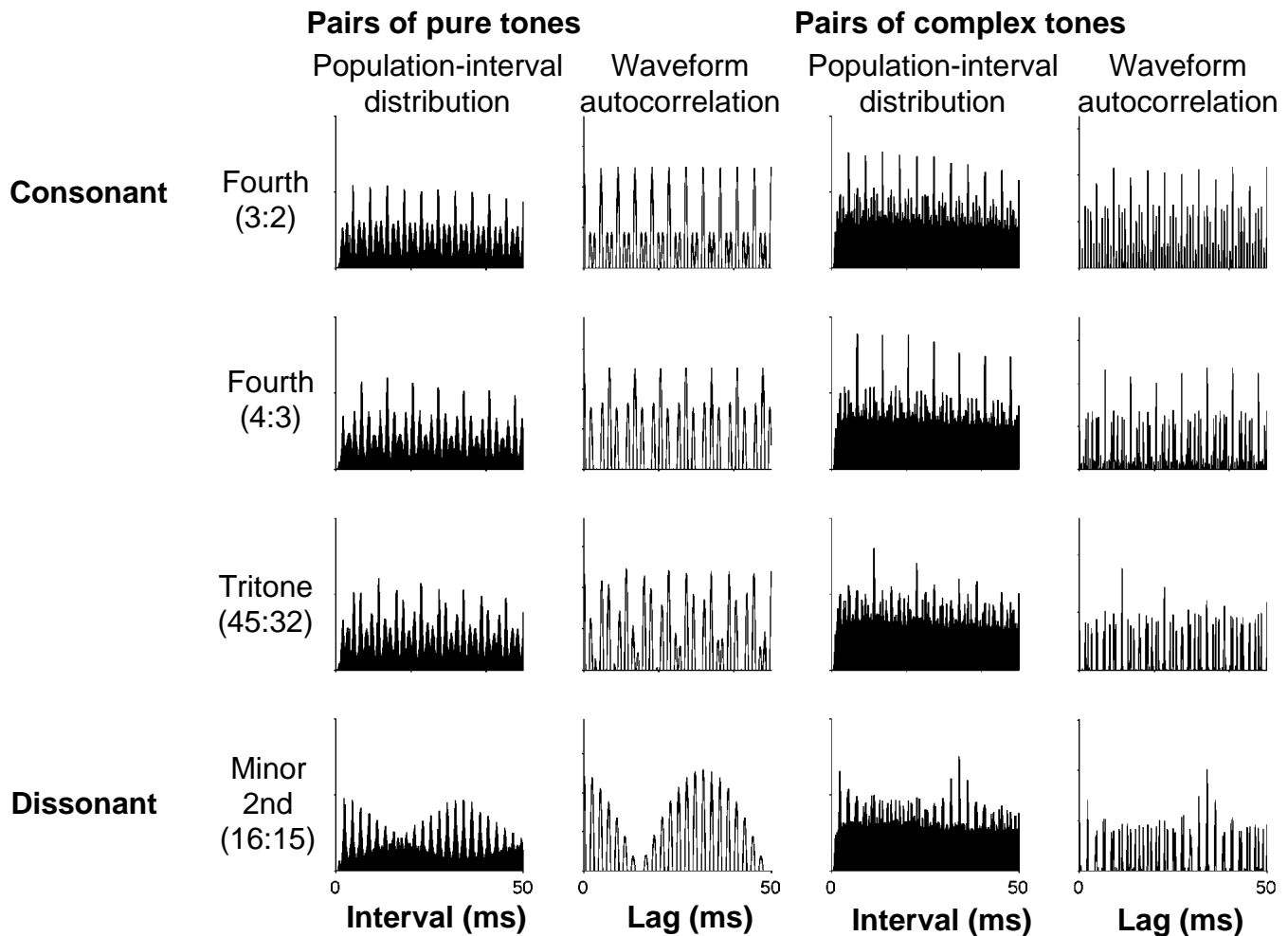


Figure 1. Comparison between stimulus autocorrelation functions and response population-interval distributions. Stimuli were pairs of pure tones or pairs of complex tones consisting of harmonics 1-6, with the lower fundamental at 440 Hz, each presented at 60 dB SPL. Positive portions of stimulus autocorrelation functions are shown. Population-interval distributions were compiled from responses of 50-100 auditory nerve fibers. Note the detailed correspondences between the positions of peaks in population-interval distributions and stimulus autocorrelations (From Cariani, Delgutte & Tramo, 1997).

## Temporal processing in neural networks

**Purely connectionist networks.** Neural networks have always embodied assumptions about neural codes. Traditionally, neural networks have assumed that sensory information is encoded via “rate-place” codes (which neurons fire how much). Connectionist nets analyze spatial patterns of excitation in their inputs to produce spatial patterns of excitation in their outputs (**place-to-place mappings**).

**Time-delay neural networks.** In the auditory system the importance of time structure for encoding the form and location of sounds has long been appreciated. Consequently the first neural networks that were proposed for auditory computations (e.g. Jeffress, 1948; Licklider, 1951) were time-delay neural networks (TDNN's).

These networks used arrays of tapped-delay lines and coincidence counters to implement cross- and auto-correlation operations on their temporally-coded inputs. Other time-delay networks employ arrays of oscillators. Time-delay networks are generally used to convert timing patterns into spatial excitation patterns (**time-to-place mappings**), such that subsequent central processing is realized using purely connectionist networks. In both connectionist and time-delay approaches, auditory matching tasks are performed by comparing stored spatial excitation profiles with incoming ones. More recently time-to-place transformations that utilize the modulation-tuning properties of central auditory neurons rather than coincidence detectors have been proposed (Langner & Shreiner).

**Timing networks.** Neural networks can be envisioned that operate on time structure in their inputs to produce interpretable temporal patterns in their outputs (**time-to-time mappings**). Very few models of this type currently exist. If neural timing information can be somehow be preserved and stored centrally, then purely temporal analyses of similarity and difference can be carried out by relatively simple temporal correlation operations. Such models are related to computational theories of cortical structures that utilize cortical pyramidal neurons as temporal coincidence units (Braitenberg, Abeles) rather than rate integrators. Recurrent structure is ubiquitous in the the brain, and “nets with loops” have been analyzed as feedback shift registers (McCulloch). The bottom-up:top-down pattern matching aspects are in many ways similar to adaptive resonance architectures (Grossberg). The recurrent timing aspects are most closely related to the “neural loop model” of Thatcher & John (1977). Thus far the functional properties of medium- and large-scale (regular and randomly-connected) timing nets have yet to be explored.

Arrays of tapped delay lines & coincidence detectors

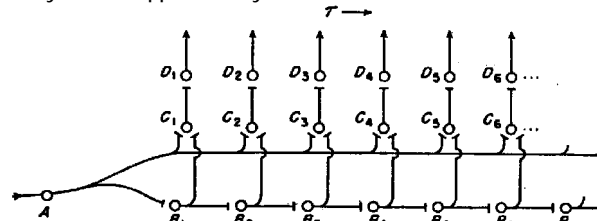
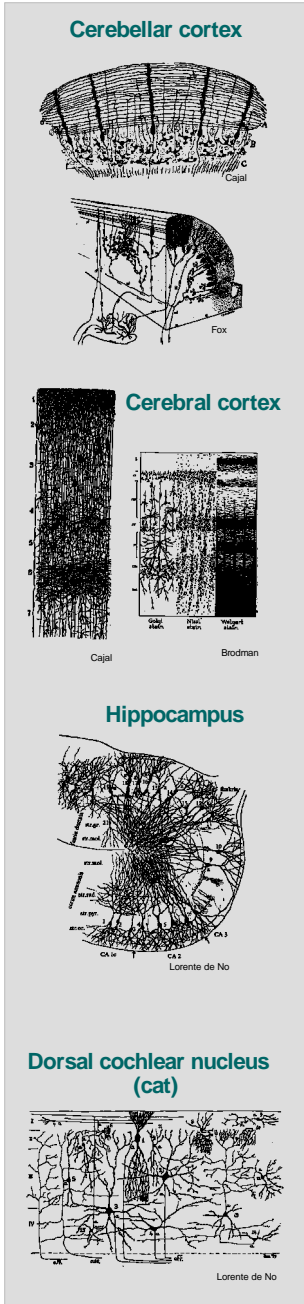


Fig. 1. - Basic schema of neuronal autocorrelator. A is the input neuron, B<sub>1</sub>, B<sub>2</sub>, B<sub>3</sub>, ... is a delay chain. From (Licklider, 1951).

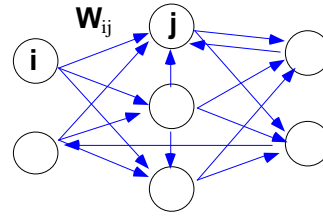
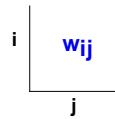
# Three general conceptions of the nature of information processing in cortical structures



## purely spatial correlators traditional connectionist nets

inputs: spatial structure  
no temporal microstructure  
elements: discharge rate integrators  
outputs: spatial activation patterns

synaptic weights



Examples: Many connectionist models  
Adaptive resonance networks  
Pitch models: connectionist versions of spectral pattern models for pitch  
Barucha; Cohen et al (SPINET)

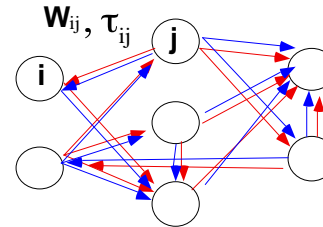
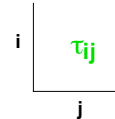
## spatio-temporal correlators time-delay neural nets

inputs: spatial structure  
temporal microstructure  
elements: coincidence detectors  
outputs: spatio-temporal patterns

synaptic weights



interneuronal delays



Examples: Jeffress binaural cross-corr.  
Licklider, Cherry: auto- & cross-corr.  
Braitenberg: cerebellar timing model  
MacKay: adaptive timing model  
Tank & Hopfield: plus many more recent implementations

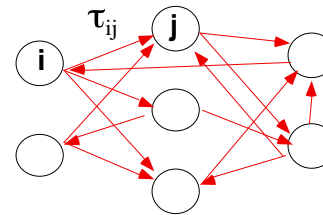
## temporal correlators timing nets

inputs: spatial structure  
temporal microstructure  
elements: coincidence detectors  
outputs: time patterns

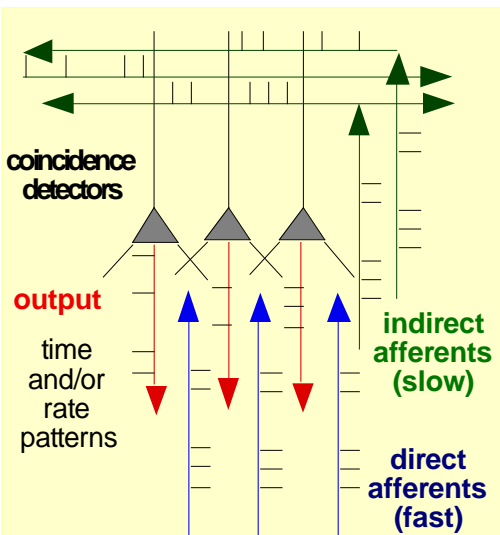
synaptic weights



interneuronal delays



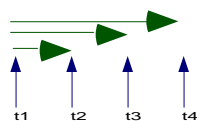
Some related approaches:  
Longuet-Higgins: temporal correlations  
Pratt: axonal parsing of spike trains  
John & Thatcher: hyperneuron model  
Reitboeck: visual scanning models  
Abeles: synfire chains



## Basic operations for timing nets

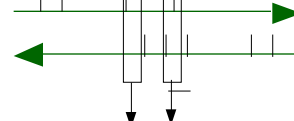
### 1. motion detection

coincidence between fast & slow inputs

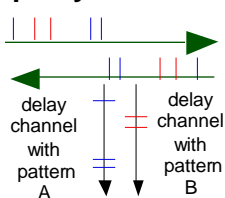


### 2. cross-correlation (AND)

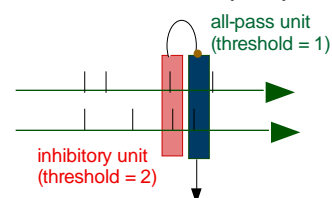
coincidence windows



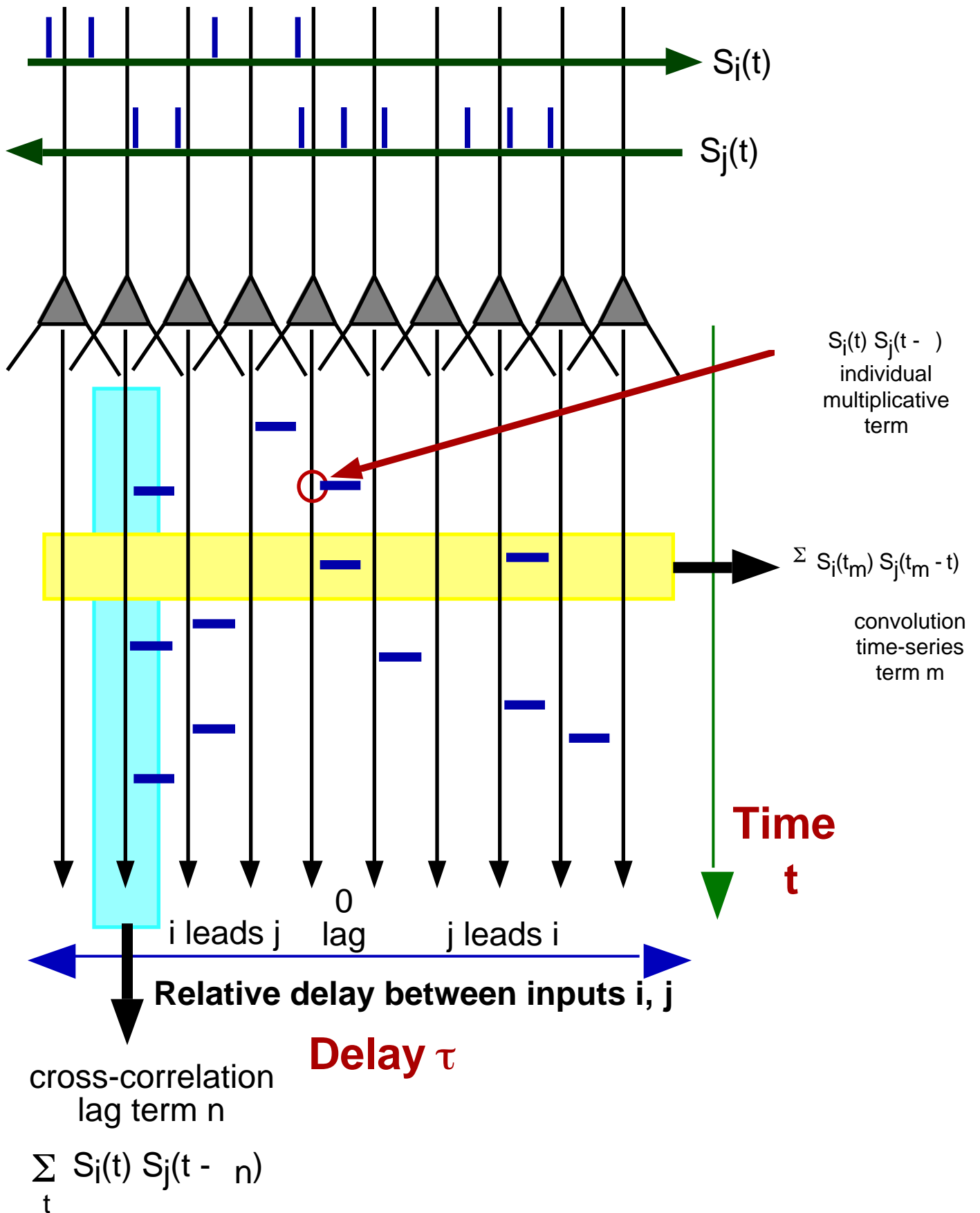
### 3. disparity detection



### 4. anti-correlation (XOR)



# Correlation, convolution, and joint autocorrelations using coincidence detectors and tapped delay lines



Consider an array of coincidence detectors that have inputs from two sets of tapped delay lines arranged in antiparallel orientation. All relative delays within a limited temporal overlap window, the conduction time across the array, are realized. Each coincidence detector requires nearly simultaneous arrival of a spike in both lines in order to fire. Consequently each spike in the output of the coincidence array represents the joint occurrence of spike arrivals in the two inputs (or multiplication of binary inputs).

Several basic computations can be carried out:

## 1. Cross-correlation function

$$\text{Corr}(\tau) = \sum_t S_i(t) S_j(t - \tau)$$

Sum # spikes in each delay channel to form rate profile as function of relative delay

## 2. Convolution function

$$\text{Conv}(t) = \sum S_i(t) S_j(t - \tau)$$

Sum # spikes at each time-step, across all delay-channels to form a time-series

## 3. Population-autocorrelation function

$$\text{PopACorr}(T) = \sum_t \sum_{\tau} [S_i(t) S_j(t - \tau)] [S_i(t) S_j(t - \tau) - \langle S_i(t) S_j(t - \tau) \rangle]$$

Sum all-order intervals present in all relative delay channels to form population-interval distribution of output.

## Use of a coincidence array to extract common pitches

The coincidence array shown above computes the joint interval distribution on the two inputs, since

- 1) only all-order intervals common to both inputs are found in the output and
- 2) all combinations of intervals present in the two input spike trains are tested by the array, provided that they arrive within the limited time overlap window.

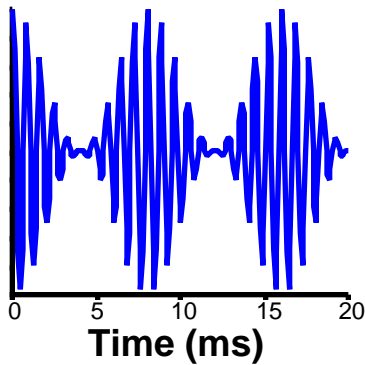
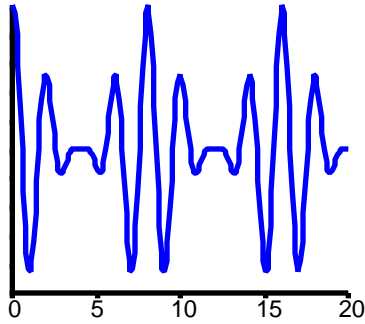
Thus a periodicity must be present in both inputs to be represented in the output, and if there is a common periodicity within the traversal time of the array (e.g. 10-15 msec), it will appear in the output of the array.

**The population-interval distribution of the output is the joint product of the population-interval distributions of its inputs (taking into account temporal contiguity).**

To the extent that the spike trains are correlated with their respective stimuli, the array outputs periodicities that are jointly present in both stimulus autocorrelation functions.

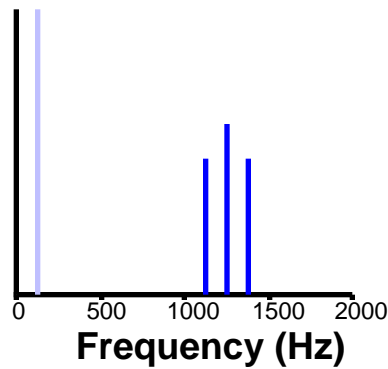
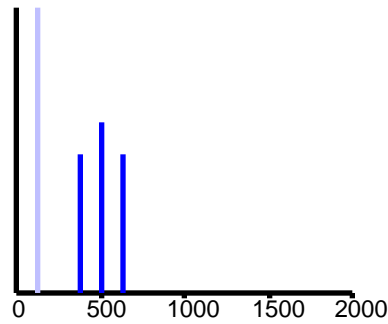
With few exceptions, the highest peaks in stimulus autocorrelation functions and population-interval distributions correspond to the pitches that are heard. The highest peaks in the joint product of the input distributions will therefore also correspond to the same pitch.

## Waveforms



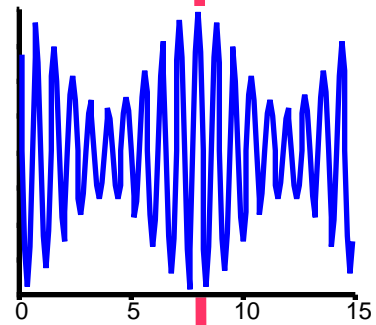
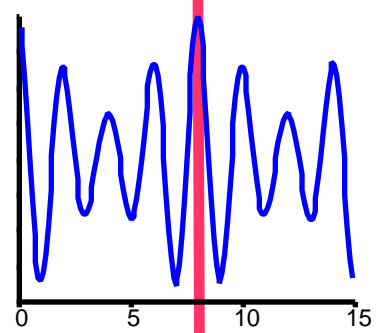
## Power Spectra

Pitch frequency,  $F_0$

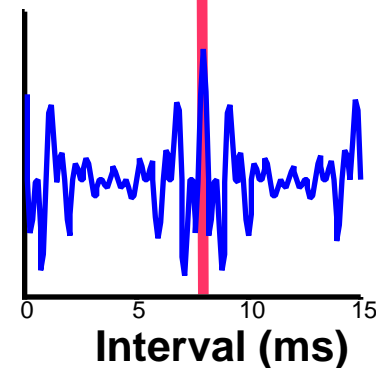


## Autocorrelations

Pitch period,  $1/F_0$



Autocorrelation of output of the coincidence array



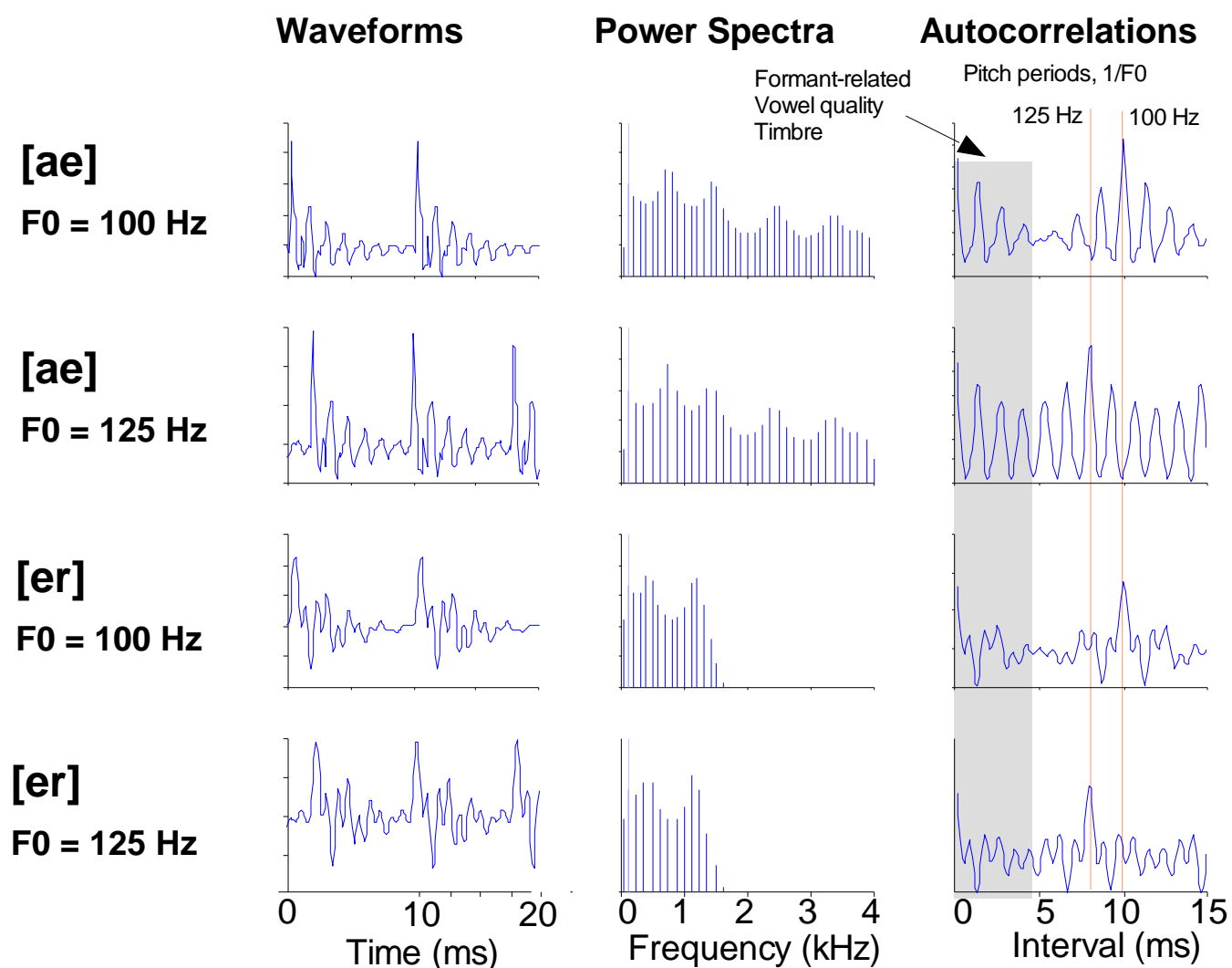
**Stimuli: AM Tones,  $F_m = 125$  Hz**  
**Top:  $F_c = 500$  Hz**  
**Bottom:  $F_c = 1250$  Hz**

The AM tones have no harmonics in common, but they produce a common low pitch at their "missing fundamentals" ( $F_0 = F_m = 125$  Hz).

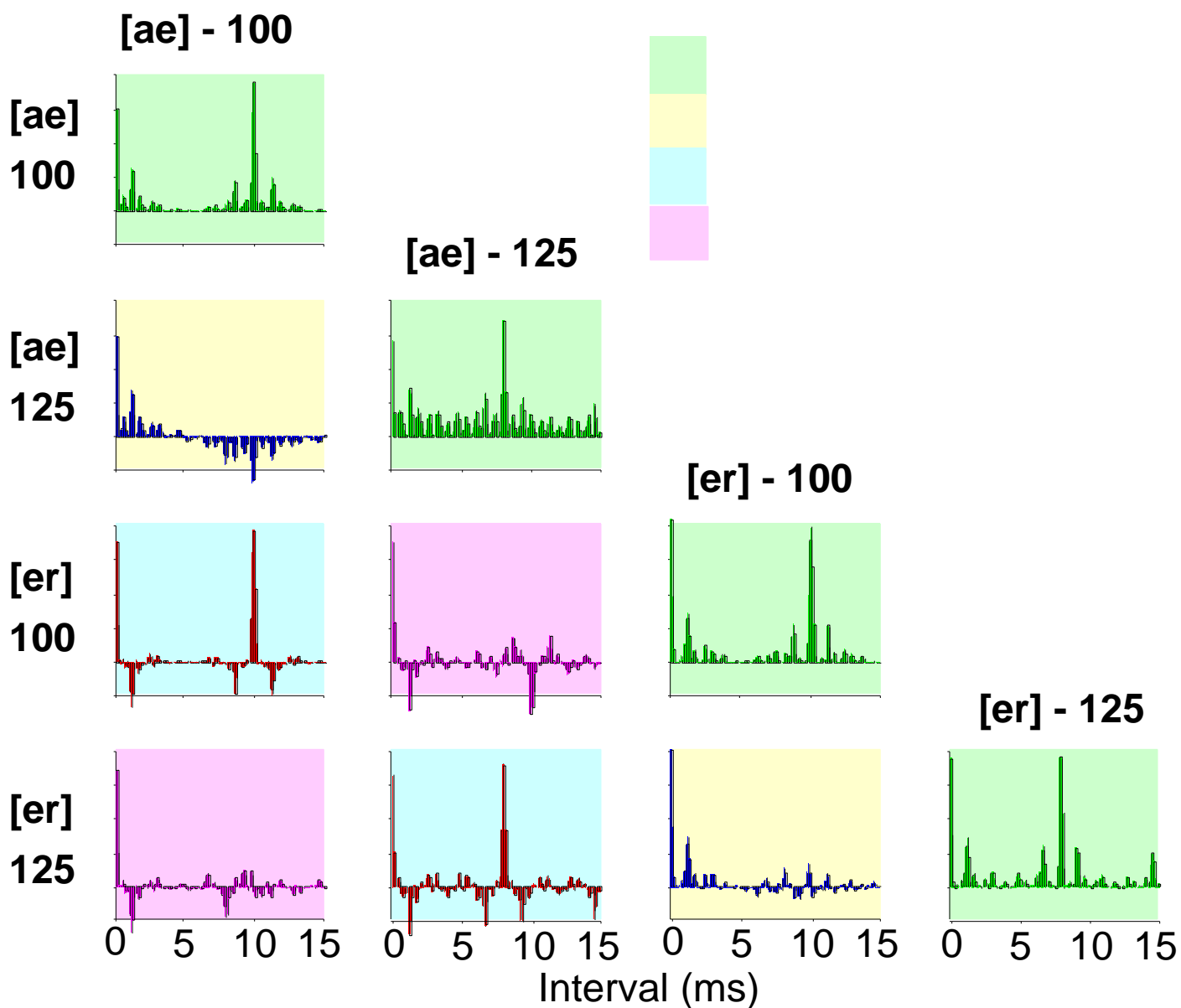
The coincidence array outputs periodicities that are common to both inputs, so that the predominant interval in the output of the array is at the common fundamental period (their common pitch period).

## Use of a coincidence array to extract common timbre irrespective of pitch

- Stimuli are 4 vowels formed from combinations of different formants & fundamental frequencies.
- Different formant structures evoke different vowel qualities, timbres.
- Different fundamental frequencies (F0s) evoke different voice pitches.
- Vowel pairs were run through the coincidence array to compute output population autocorrelations.
- Periodicities in the output of the array correspond to common F0s and/or formant structures.
- The array extracts common pitch irrespective of timbre & common timbre irrespective of pitch



# Population autocorrelations of the output of a coincidence array for all vowel combinations

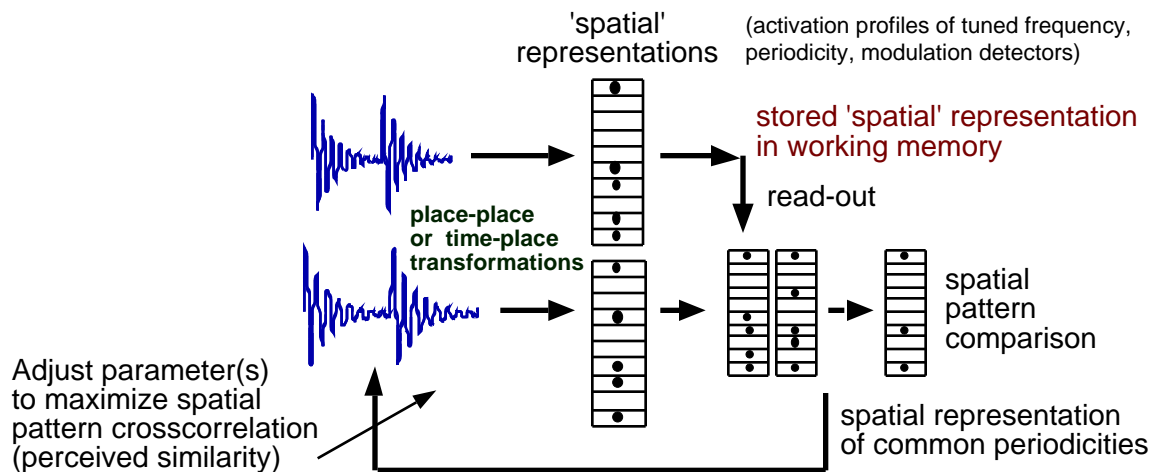


# Stimulus-matching using temporal pattern codes, temporal memory traces, and coincidence nets

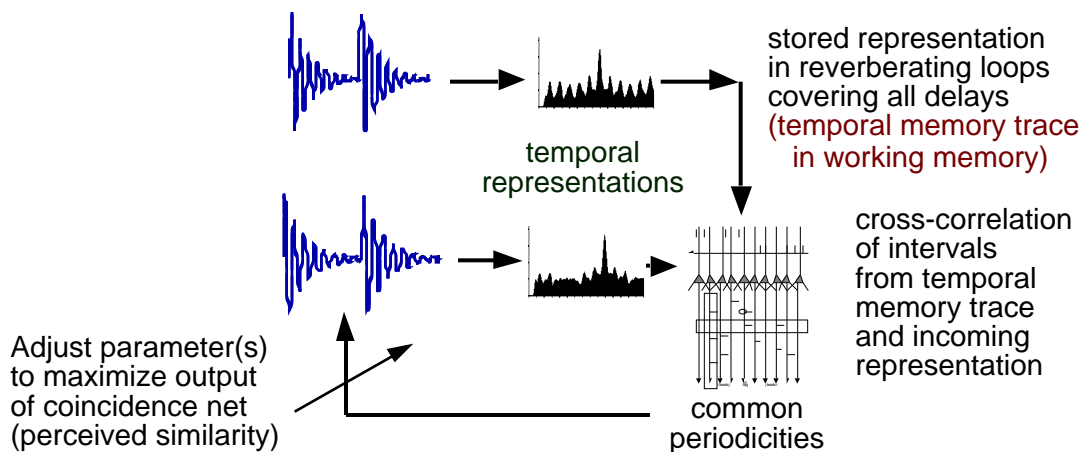
We have outlined above how two sets of temporal patterns (interval statistics or post-stimulus time patterns) can be compared in coincidence arrays in order to extract pitch and/or timbral similarities. These mechanisms could provide a general basis for the recognition of auditory forms (e.g. recognition of common pitch irrespective of timbre for speaker identification and recognition of timbre irrespective of pitch for identification of musical instruments).

However, in order for such global temporal mechanisms to serve such a role it is necessary to postulate the existence of **temporal memory traces**, i.e. means of storing time patterns in a reverberating working memory such that they can be compared with incoming ones.

**Stimulus matching using spatial memory patterns.** Traditionally, information-processing models of stimulus-matching have assumed that sensory information is centrally represented and stored in 'spatial' or across-neuron activation profiles of ensembles of neurons tuned to detect specific features of the stimulus.

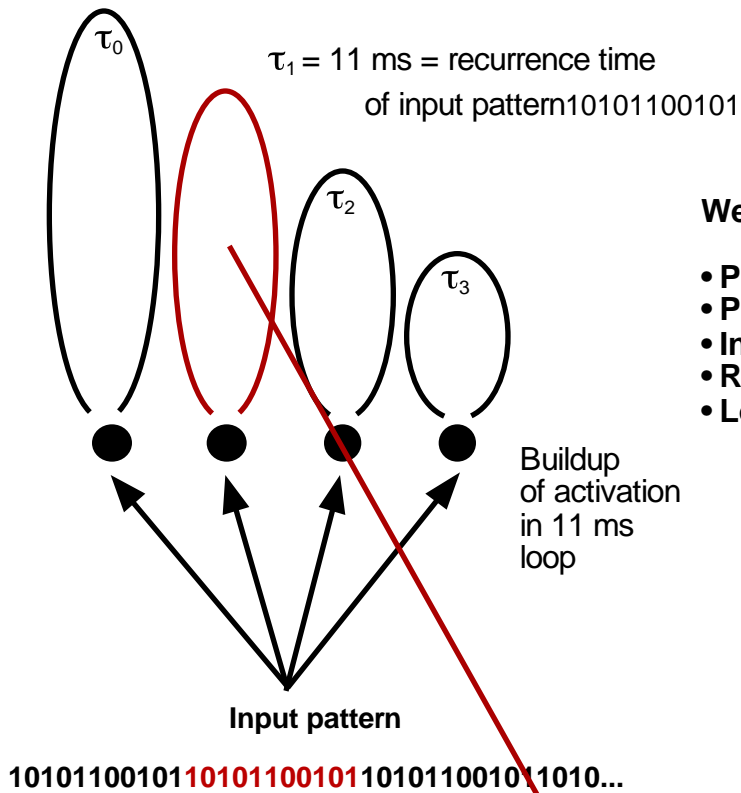


**Stimulus matching using temporal memory traces.** The alternative model proposed here holds temporal patterns in a reverberating working memory. The temporal patterns can be either post-stimulus time patterns or population-wide interval statistics. To match stimuli, the subject maximizes the output of an internal coincidence array.



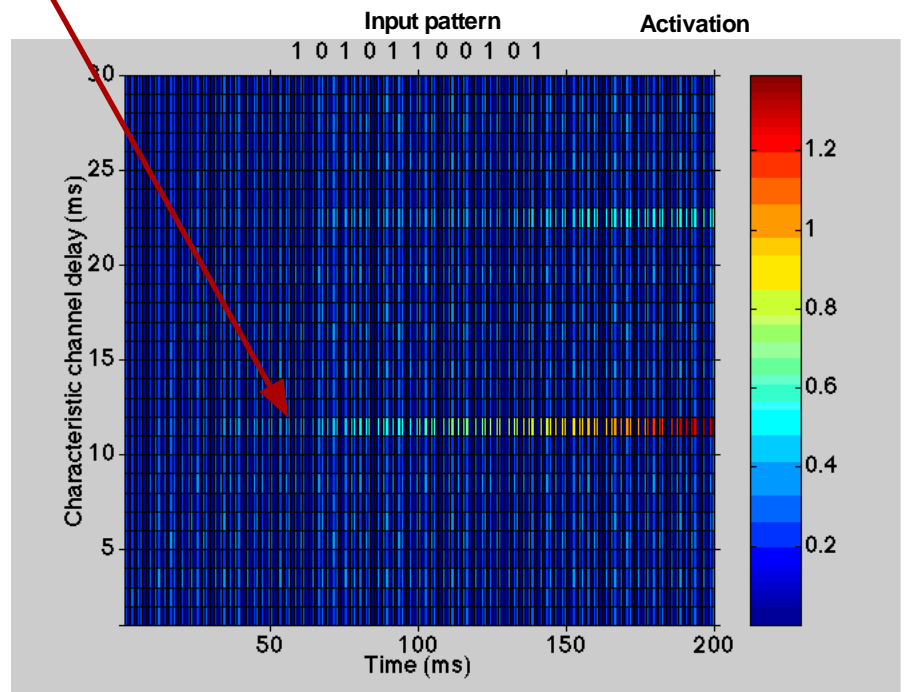
# Detection of recurrent time patterns

Pattern builds up most rapidly in channel(s) with recurrence time(s) equal to the pattern repetition period.



We have the ability to detect repeating temporal patterns on many different time scales:

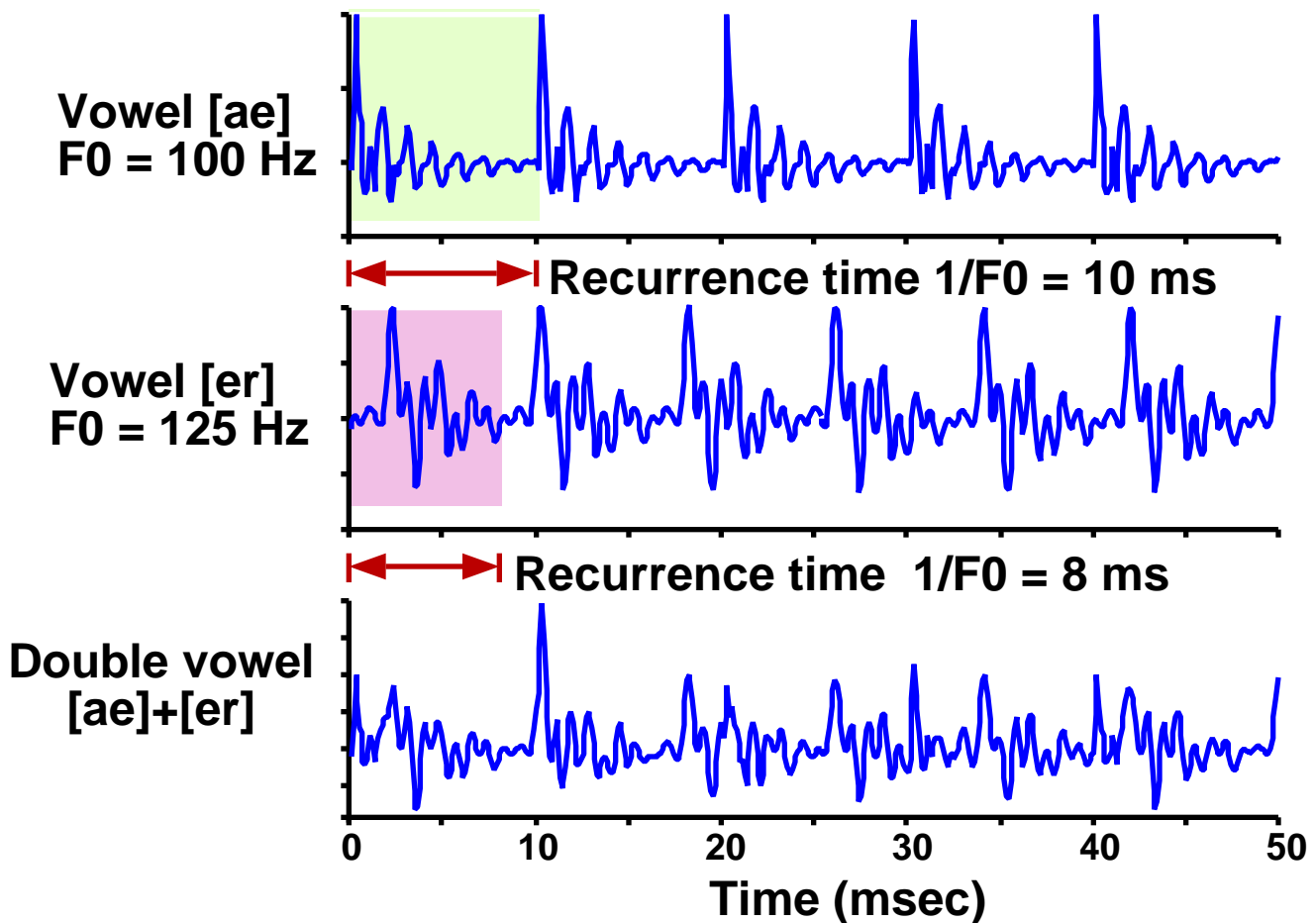
- Pitch of harmonic sounds (~1-20 ms)
- Pitch of repeated noise (same period recurs)
- Infra-pitch (~20-200 ms)
- Rhythmic patterns (~200-2000 ms)
- Longer arbitrary patterns (many seconds)



# Separation of multiple recurrent time patterns

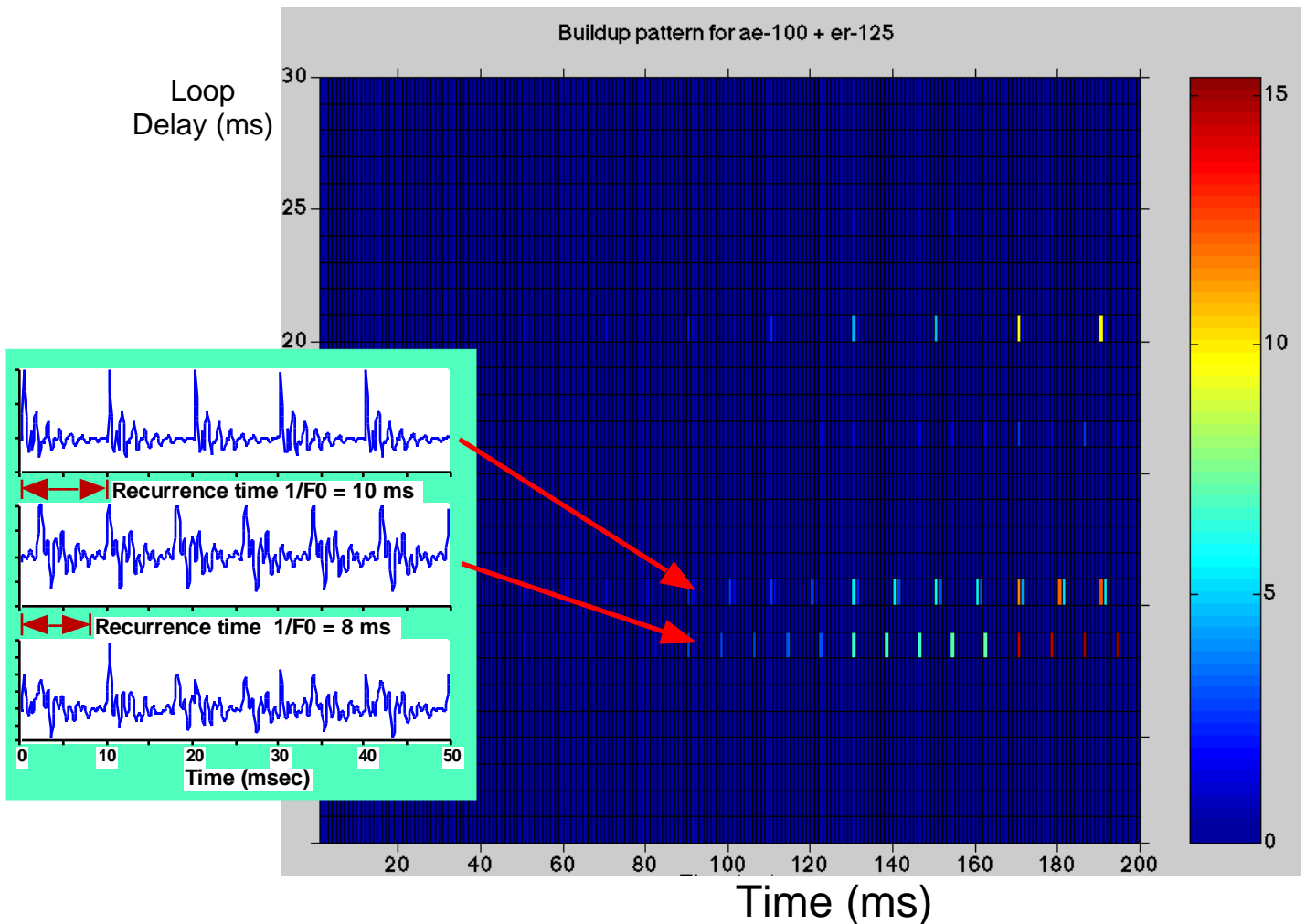
## Separation of two vowels with different F0's

Consider two vowels, ae and er that have different fundamental frequencies at 100 and 125 Hz respectively. Each vowel has its own constant waveform pattern that recurs each fundamental period, but the relationship between the waveforms of the two vowel periods is constantly changing. Thus each vowel has its own internal invariant waveform pattern, while the relations between the two vowel waveform patterns change.



Two vowels ae-100 & er-125 were processed through the simple recurrent timing network outlined above. The vowels were decimated down to a 1 kHz sampling rate, half-wave rectified, and added together.

Each vowel pattern builds up in the delay loop whose recurrence time matches its fundamental period. If multisynaptic loops are permitted, then coincidence elements can participate in multiple delay paths and support buildup of time patterns associated with multiple objects (multiplexed representations).



## General strategies for sound separation

A very general hypothesis about auditory grouping would hold that sets of stable phase-relations fuse together into unified objects, whereas unstable phase-relations segregate into different streams.

Recurrent timing networks accomplish this grouping of common time patterns by providing many delay paths through which successive incoming time patterns can be compared such that similar patterns contribute to the build-up of their common pattern within the network. Such coding and scene analysis mechanisms operate directly on the phase structure of the sound encoded through phase-locked discharges. Explicit detection and binding of local features is not needed.

## Conclusions

While the examples considered here are certainly very rudimentary, they nevertheless afford us glimpses of the kinds of perceptual computations that can be realized out using temporally-coded inputs fed into arrays of delay lines and coincidence detectors.

We have demonstrated that a feedforward coincidence array can operate on two temporally-coded inputs in order to extract common periodicities that may subserve the perception of pitch and timbre. Thus for two sounds, common pitch can be recognized independent of timbre, and common timbre can be recognized independent of pitch. Further, both of these operations can be realized using the same, simple mechanism.

We have proposed recurrent timing networks in which time patterns are stored as temporal memory traces. We have demonstrated how periodic time patterns can build up in these networks such that they can be detected. We have demonstrated how multiple time patterns with different recurrence times (fundamental periods) can be separated in such networks.

Some potential computational advantages of these networks are 1) no explicit time measurement is involved, so that no highly tuned delay lines or periodicity detectors are needed, 2) precisions of representations and comparisons reside in spike timings rather than in spatial activation profiles of tuned elements, 3) harmonic relations implicit in interspike intervals are preserved, and 4) population-wide operations that make use of all neural responses, even weak ones, obviate the need to select relevant subpopulations for analysis.

Through rich sets of delays, recurrent timing networks can differentially amplify multiple sets of arbitrary recurrent time patterns. This points to an alternative strategy for scene analysis that does not rely on binding together ensembles of local features into stable objects. Instead, such networks provide general-purpose pattern recognizers that form objects by fusing invariant temporal correlation structures in their inputs.

How these computational strategies can be scaled up to large numbers of inputs, delay paths, and coincidence elements remains to be worked out. Whether these kinds of neural computations are in fact carried out in central auditory structures are empirical questions that can be only addressed through directed neurophysiological experiments.

## Temporal memory traces in the brain

There are a number of considerations that suggest the possibility of central time codes for at least some kinds of time-structured inputs. Recurrent connections that form very large numbers of delay pathways are the rule in the central nervous system (e.g. thalamocortical and cortico-cortical loops, the recurrent connectivity of the hippocampus). A great deal of temporal structure exists in virtually every sensory system (Cariani). The existence of precisely-replicated spike patterns in the cortex (Abeles, Lestienne) suggests that time structure can be preserved in populations of cortical neurons. Cortical units that assimilate input periodicities during electrical conditioning and that output those time patterns have been found (Morrell). Behavioral conditioning experiments show that animals readily generalize time patterns that are common to different modalities (e.g. 3 vs. 10 Hz click, flash, or shock trains; John). Other animal conditioning experiments show that the time structure of events extraneous to rewards is retained in memory (Miller). There are also many examples from the perception of music, rhythm, and arbitrary repeating patterns (Bregman, Jones, Pollack, Large) that suggest generalized mechanisms for registering arbitrary temporal patterns on long time scales.

## Acknowledgments

Bertrand Delgutte, Mark Tramo and I collected the auditory nerve data that was used to illustrate population-interval codes. Thanks to Martine Turgeon, Alain de Cheveigne, John Culling, Ed Large, Jennifer Melcher, and many others at the Eaton Peabody Lab for useful discussions concerning correlation, anticorrelation, auditory organization, and timing models. This work was supported by Research Grant DC03054 from the National Institute on Deafness and Other Communicative Disorders, National Institutes of Health.

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