

PERIODICITY PITCH AND RELATED AUDITORY PROCESS MODELS *

J. C. R. Licklider

Abstract

Schouten's (34-38) residue and other phenomena call for extension of place theory to account for the role of periodicity in determining subjective pitch. This paper examines several mechanisms that might be used by the auditory system to recode the information carried by the time pattern of the output of the cochlear frequency analyzer. A distinction is made between mechanisms that involve ordered arrays of components and mechanisms that involve unordered arrays. The relation of periodicity mechanisms to „property filters” is examined, and periodicity pitch is discussed in relation to „sharpening” and binaural interaction.

Introduction

During the last 25 years, the study of hearing has advanced 35 millimeters. At the beginning of the period, it was known that the cochlea performed a mechanical frequency analysis upon vibratory signals delivered to it through the middle ear or temporal bone, but neither the general structure of the process of analysis nor the exact nature of the product of analysis was clear. The analysis was the subject of speculations and conjectures. Now, largely as a result of Békésy's (2, 3) celebrated observations, the mechanical analysis is well enough understood that the speculations and conjectures have been replaced by graphs, charts, and computer models (9, 10). Investigation has shifted to later stages of the auditory process.

The process through which neurons of the auditory nerves are excited seems to be understood now perhaps a little better than cochlear mechanical analysis was understood in 1937. Basic features of the responses of neurons in the auditory nerve, and of neurons and aggregates of neurons in auditory centers of the brain, have been observed. (15, 41) However, no one now has knowledge much more advanced than „hunches” concerning the overall plan and products of the neural auditory process. The action of the auditory nervous system is therefore now the subject of approximately the same level of speculation and conjecture as the mechanical analysis was before Békésy's observations.

*) Preparation of this paper was supported in part by the Air Force Office of Scientific Research under Contract AF 49(638)-355, AFOSR 2681.

The purpose of this paper is to summarize recent ideas on one small but perhaps crucial topic, the role of periodicity in the perception of pitch. This topic has had a central position in audition, off and on, ever since the discussions of Seebeck (35), Ohm (31,32), and Helmholtz (20). Interest in the topic is now particularly great because there are enough facts to make it clear that periodicity plays a significant role in pitch perception, yet not enough facts to define the role precisely or to indicate how it is played.

By using the words „speculation” and „conjecture”, I mean to convey not a negative evaluation of the ideas to be summarized but a qualification: a declaration of tentativeness and a warning of probing beyond established facts. The word „theory”, it seems to me, is also appropriate, but only after a distinction is made between the present hypothetical, heuristic kind of theory intended to facilitate discovery (and thereby almost surely get itself disproved), and the rarer synthetic, consolidating kind of theory, intended to organize established facts and facilitate their incorporation into the body of knowledge.

PERIODICITY AND FOURIER FREQUENCY

The period of a sinusoidal wave is so well known to be the reciprocal of the frequency of the sinusoidal wave, and we are so accustomed to thinking in terms of frequency, that periodicity may seem at first thought to be only the other face of a familiar coin. Usually it is. A necessity for making a further distinction between periodicity and frequency — further than that „the period is the reciprocal of the frequency” — arises, however, when we consider certain compound (nonsinusoidal) waveforms. The waveform in Fig. 1A, for example, is periodic with period T , yet it contains no power at the Fourier frequency $f = 1/T$. Thus the wave has a definite periodicity not corresponding to any frequency energetically present in the spectrum. Clearly, the periodicity suggests things that are not suggested directly by the frequency composition **per se**. Even to a beginning student (or perhaps particularly to a beginning student), the waveform suggests that the stimulus will give rise to a sensation similar in pitch to that produced by a 200 Hz tone, whereas the spectrum seems to suggest that the pitch will be high.

The waveform in Fig. 1B is not itself periodic, but its envelope is periodic with period T . The waveform of 1B itself has no power at the Fourier frequency $f = 1/T$. It is of interest to deliver to the ear waveforms such as those of 1A and 1B and to examine the subjective experiences to which they give rise.

„PLACE PITCH” AND „PERIODICITY PITCH”

Place Theory

Because the „place theory” has been dominant for so long a time, and because periodicity mechanisms are subsequent (if not secondary) to place mechanisms in the auditory process, we need a fairly definite statement of the place theory of pitch perception to use as a point of departure. The statements made by Helmholtz (20) and other classical place theorists seem to me not to be entirely appropriate for that purpose; they are too far re-

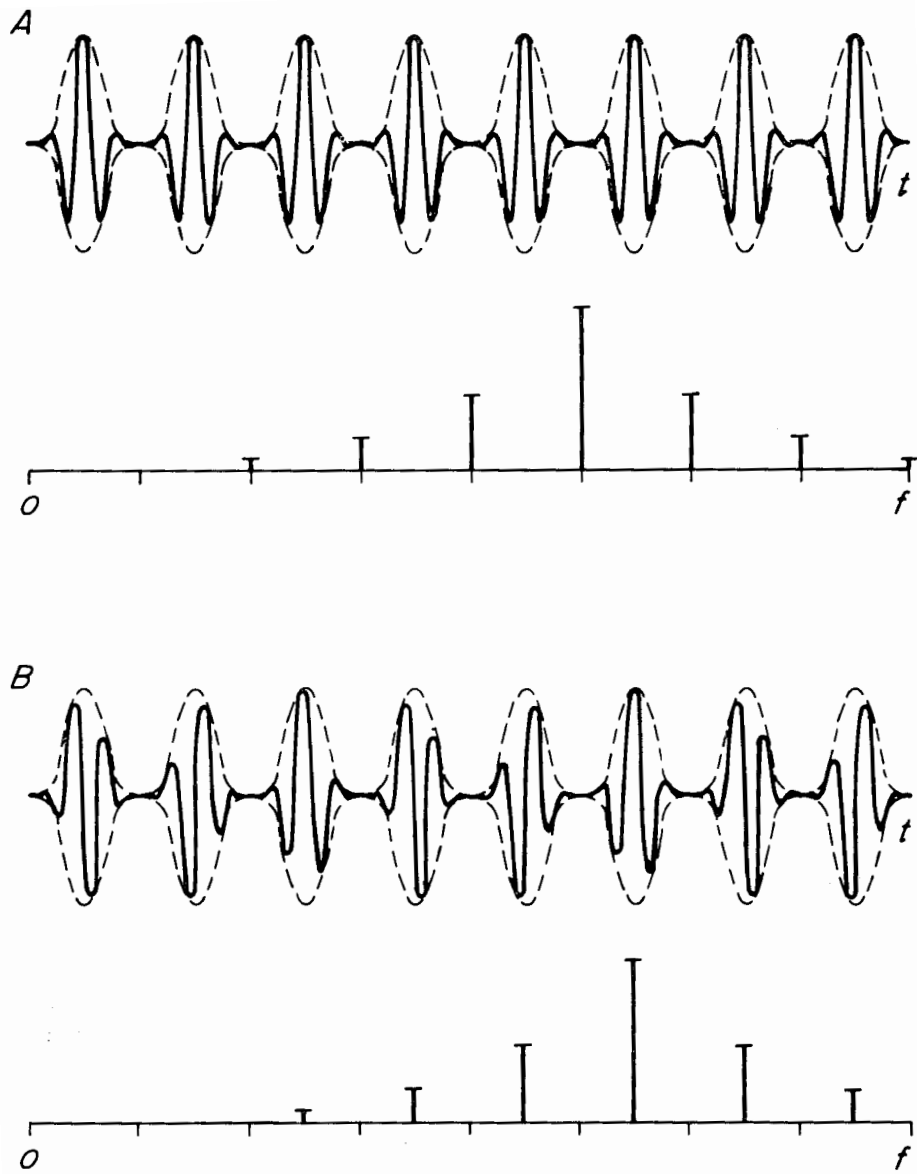


Fig. 1. Periodic waveforms illustrating distinction between frequency and the reciprocal of period. The waveform of A is periodic with period T, but (as the spectrum below it shows) contains no power at frequency $f = 1/T$. The envelope of the waveform of B (but not the waveform itself) is periodic with period T. The spectrum corresponding to the waveform has no power at $f = 1/T$; the spectrum corresponding to the envelope has.

moved from the modern context. Perhaps it would be helpful for the statement to mention specifically the cochlear partition (or the basilar membrane) and to make less specific reference to a „perceptual” region of the brain:

1. To each frequency along the frequency scale of the running spectrum of the stimulus there corresponds a point along the length of the basilar membrane. The mechanical action of the cochlea distributes each frequency component of the running spectrum over an interval about the corresponding point. The intervals are broad, especially for low-frequency components. The transformation is approximately linear for stimuli of low intensity.

2. To each point along the basilar membrane, there corresponds a point along a continuum of neural tissue in a „perceptual” region of the nervous system. The nervous system maps the basilar membrane onto the perceptual continuum in such a way as to preserve ordinal relations. The neural transformation is a „projection”: local facilitatory and inhibitory interactions may modify (particularly, sharpen) the distribution of activity, but remote interactions are weak relative to local ones.

3. To each point along the continuum in the perceptual region of the nervous system there corresponds a point along a continuum of subjective pitch. In instances in which activity is concentrated about one or a few points on the neural continuum, subjective pitches arise at (or about) corresponding points on the pitch continuum. In instances in which activity is uniformly distributed over the neural tissue, either no subjective pitch arises, or a subjective pitch arises that depends upon some weighting of the activities at various points along the neural continuum.

4. An influence called „attention” may affect the coefficients („gains”) of the projection channels and the strengths of the local interactions in the projection mechanism. It may also (at the discretion of the theorist) affect the coupling between the perceptual continuum in the nervous system and the subjective pitch continuum.

5. Therefore, a single concentration of energy along the frequency scale of the running spectrum gives rise to a corresponding single pitch. If there are several or many concentrations of energy along the frequency scale, there may be several pitches or only one pitch, depending upon the states of the projection mechanism and attention. In any case, the pattern in pitch deviates from the pattern in frequency only in ways that can be attributed to facilitatory and inhibitory interactions that are predominately **local** in a **unidimensional** (but possibly multi-level) projection system.

The foregoing formulation of place theory of course involves concepts that did not appear explicitly in the writings of the classical place theorists. It represents an attempt to extend the classical theory into the present context, to be specific where specificity is warranted and to be general (or vague) where neither the classical theory nor the current situation provides a basis for making a specific choice.

In the formulation, there is no reference to the fine timing of events within the temporal resolution of the running spectrum. That is to say, place theory, as here stated, is indifferent to timing finer than about 0.1 sec. It therefore ignores the basis of anything that might be called „periodicity pitch”. Its pitch is „place pitch” — pitch related to place of excitation or activation.

Phenomena Difficult to Explain Through Place Theory

The present difficulties of „pure“ place theory are caused almost entirely by two phenomena, Schouten's (34-38) residue phenomenon and Huggins' (28, 8) binaural-pitch phenomenon.

Since the residue phenomenon was elucidated in the preceding paper, I shall not discuss it in detail here. The essential points are:

1. A low subjective pitch may be associated with the middle-or high-frequency components of a compound, line-spectrum stimulus, even when no corresponding frequency component is energetically present in the stimulus.
2. The residue is distinguishable subjectively from the fundamental tone or difference tone that is introduced (if the sound pressure level is high) by nonlinear distortion in the middle ear or pre-neural cochlear mechanism (37). The residue may be heard simultaneously with the fundamental or difference tone. (37).
3. The low pitch of the residue persists even though the low-frequency channels are saturated with random masking noise (27, 43). Thus, in direct contradiction of pure place theory, a low pitch may be heard through high-frequency cochlear channels.

The chief counter-argument used in response to the difficulty presented by the residue has been that the „missing fundamental“ or a difference-frequency component, though perhaps not present in the acoustic stimulus, is introduced by nonlinear distortion at some stage prior to the part of the auditory (cochlear) process in which the various frequency components are distributed to their proper channels. This counter-argument was used by Helmholtz (20), Fletcher (12, 13), Hoogland (21), and many others. Unless counter-counter-evidence is at hand, the counter-argument is effective against point 1 (above). However, Schouten (37, 38) had, and has, good counter-counter-evidence. The counter-argument is ineffective against points 2 and 3 (above). In my opinion, the conclusion concerning low pitches without low frequencies should be that:

- a. Under some circumstances, the „missing fundamental“ (or difference tone) is reintroduced by nonlinear distortion, and the reintroduced component accounts for the (low) pitch reported.
- b. Under other circumstances, nonlinear distortion contributes, but the low pitch is due also in part to time-patterned activation of middle- or high-frequency channels.
- c. And under still other circumstances, perhaps only under the special circumstances of carefully planned experiments, all spurious contributions assignable to low-frequency channels of the cochlear output are accounted for or eliminated, and low pitch arises through high-frequency channels.

Thus the conclusion at this point is **not** that the place-theory mechanism should be discarded, or that it never accounts for the facts. The conclusion at this point is only that there is one kind of observation that pure place theory (as formulated) is inadequate to explain, and that place theory therefore needs to be extended.

In the Huggins (28) phenomenon, or Huggins-Cramer phenomenon, since now it has been explored systematically by Cramer and Huggins (8), pitch arises from a binaural interaction.

The stimulus presented to the listener's left ear is a random noise with uniform spectrum. Alone, it has no very definite pitch. It sounds like „shh...”. The stimulus presented to the listener's right ear is also a random noise with uniform spectrum. Alone, it sounds quite like the other. However, the two random noises have been derived from a common source. They are alike and in phase up to some frequency $f_c - \Delta f$ and above $f_c + \Delta f$. Between $f_c - \Delta f$ and $f_c + \Delta f$, however, the two noises are unlike in respect of the phasing of their components. When the two noises are presented together, one to the left ear and the other to the right, the listener hears a faint tone, deep in a noisy background. He can report its pitch, which depends upon f_c and is appropriate to it.

The phenomenon just described is limited to values of f_c below about 1400 cps and to values of Δf worked out by Cramer and Huggins. For classical place theory, it poses an embarrassing problem, for the theory purports to define the physical and/or physiological correlates of subjective pitch, the theory says nothing about binaural interaction, and here is a controllable low pitch arising through binaural interaction from stimuli that monaurally are nothing but random noise. Note, however, that — like the residue — the Huggins-Cramer phenomenon calls not for a rejection but only for an extension of place theory.

POSSIBLE MECHANISMS FOR PERIODICITY PITCH

There appear to be two main approaches to the study of neural processes: (1) to examine the nervous system (with electrodes, dyes, etc.) and see what it suggests, and (2) to guess what objective the nervous system is trying to achieve, to consider various techniques for achieving that objective, and then to examine the nervous system and see whether it appears to be using any of those techniques. Most researchers use a mixed strategy, but I think Professor Békésy and many physiologists seem to favor approach (1), which gets immediately to the question at hand, whereas many engineers, psychologists, and psychophysicists prefer (2), which offers them an opportunity to bring their own special knowledge to bear upon the development of a theory before nature has a chance to prove the theory wrong. In any event, we are involved here in approach (2).

The process that transforms the pattern of the mechanical vibration of the basilar membrane into a pattern of discharge of neurons in the auditory nerve has at least one feature of great significance in connection with periodicity pitch. The excitation of neurons is inherently a nonlinear process similar to rectification. It is sensitive, therefore, to frequencies not energetically present in the vibration of the membrane, and it converts „missing fundamentals” into frequencies of neural discharge just as well as it does „present fundamentals”. The crucial point is, of course, that it sets up a train of discharges at the frequency of a missing 200-Hz fundamental, for example, in bundles of neurons that constitute middle- or high-frequency channels, and not in the bundles that would be excited by energetic sinusoidal vibrations near 200 Hz. Our problem, therefore, is to extend or modify the place theory in such a way that trains of impulses at 200 cps in middle- and high-frequency channels

of the auditory nerve can give rise to, or contribute to, a low subjective pitch.

At the present time, neural signals are usually thought of either as (a) trains of nerve impulses in axons or axon bundles or as (b) complexes of „spike“ and „local“ potentials (together with associated chemical activity) in the cell bodies, dendrites, and axons of neurons in central nuclei plus the „slow“ potentials that are recorded throughout central nuclei. Neurons themselves are recognized to be quite complex and diverse, and neuronal networks, extremely complex and diverse. There is no dearth of components with which to synthesize hypothetical processing systems.

Despite the richness of possibilities for detailed configuration, there seem to be only a few basic operations for discrimination of periodicity. Any one of them could be applied in a thousand particular ways to the task of discriminating the periodicities in the cochlear output, but fortunately it may not be necessary to list the particular manifestations in order to sensitize oneself to evidence of one of them in experimental data.

Time-Domain Representation

The first general possibility is that periodicity remains encoded in the time domain until the signals leave the auditory system. This amounts to saying that the ultimate neural variable underlying subjective pitch is frequency of neuronal discharge. It does not entirely avoid the problem of transforming the message out of the time domain, for such a transformation must be made before there can be a selective verbal (or other motor) response.

In any event, this first general possibility has two subpossibilities: (1) that periodicity is simply preserved, more or less accurately, but without reduction of impulse repetition rate, and (2) that pulse-count division or pulse „frequency scaling“ is employed. The volley mechanism of Wever and Bray (45) is of course the mechanism of choice for (1), but the measurements of Goldstein and Kiang (19) underscore the conclusion that the highest centers of the auditory system do not “follow frequency” beyond about 200 Hz. In as much as the „average response“ technique used by Goldstein and Kiang is responsive to frequency-scaled as well as unscaled impulsive responses, so long as they are time locked, their failure to find time-locked cortical responses to high-frequency stimulus pulse trains argues against simple frequency-scaling hypotheses, also. My feeling, therefore, continues to be that „time domain all the way“ is not promising, either as a substitute for or as an extension of place theory.

Accumulating evidence that the cortex is not essential for frequency discrimination suggests that we keep open the hypothesis that, up to 1000 or even 2000 pulses per second, neural frequency or periodicity may be effective at the thalamic level. We might look there, just as well as at lower levels, for a periodicity-to-place transformation. But that takes us out of the category of time-domain representations.

Periodicity-To-Place Transformation

The second general possibility is that the information carried in the periodicity or fine time structure of the cochlear output is transformed into the „place domain“ at some stage, presumably a fairly early stage, of the auditory

process. Again there are two sub-possibilities: (1) that the transformation is one that maps neural frequency into a definite dimension of the neural tissue, a dimension that underlies or corresponds to subjective pitch, and (2) that the transformation merely allocates different frequencies to different neurons, the locations of which are significant, not in relation to any definite dimension or coordinate system, but only through interconnections with other neurons in a system that, insofar as macroscopic spatial arrangement is concerned, appears more or less random.

The task of a „periodicity-to-place” transformation system is to accept a single function of time and to produce a time-varying pattern in one or more spatial dimensions. In the input time function, two different levels or orders of time are significant, „gross” time and „fine” time. The fine structure of the waveform may be regarded as undergoing slow variations, as varying in gross time. The changes of the output pattern must be slow changes; the output pattern must vary in gross time. Each momentary spatial pattern of the output signal must be a representation, in some form, of the fine structure in a corresponding segment of the input wave. Perhaps the most widely familiar „periodicity-to-place” converter is extremely simple in principle: the cathode ray oscilloscope.

Other more-or-less familiar systems for making transformations of the type discussed are:

1. A filter bank — an ordered array of band-pass, low-pass, high-pass or other filters;
2. A Fourier transformation system — an ordered array of correlators with reference signals supplied by a corresponding array of oscillators;
3. An autocorrelation system — an ordered array of correlators with reference signals derived from the input signal through successive taps on a delay line;
4. A power-series transformation system — an ordered array of correlators with reference signals supplied by direct-current, ramp, parabola, cubic, etc., generators.

Note that the cathode-ray oscilloscope and the power-series transformation system have an intrinsic tendency to break the input wave up into segments and represent the segments successively as „frames”. Filter banks, Fourier transformers, and autocorrelators, on the other hand, more-or-less naturally yield representations that develop continuously and progressively in gross time. Although the advantage is hard to evaluate, the continuous-gross-time feature favors the latter schemes for applications in auditory theory.

Filter-Bank Model

Because the excitation of nerve impulses is inherently nonlinear, a neuronal network would have to be rather complex to simulate closely the behavior of a linear wave filter. However, with quite simple arrangements of idealized neurons one can achieve interesting patterns of frequency selectivity. Is it not conceivable that the nervous system might use arrays of simple neural filters to transform patterns in the frequency or periodicity of auditory nerve discharges into place patterns?

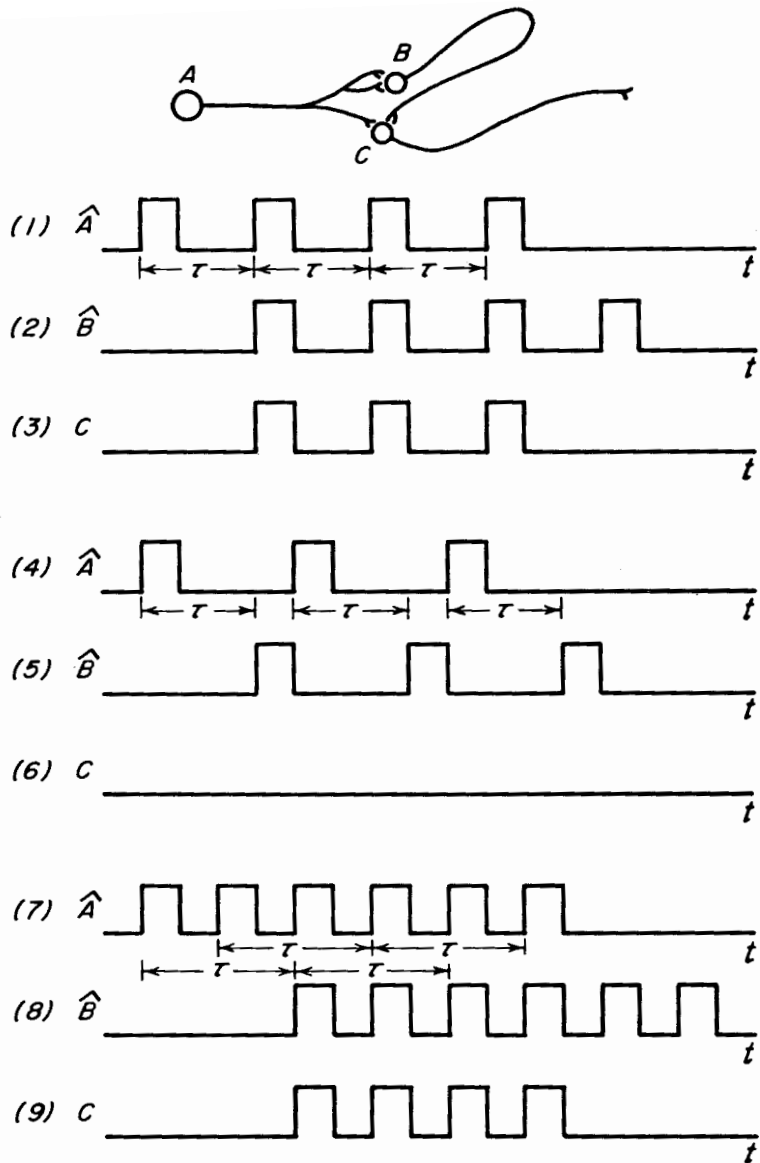


Fig. 2. Frequency-selective neuronal network. \hat{A} is the signal (schematized) at the input axon end-brush. \hat{B} is the signal at the auxiliary axon end-brush. C is the signal at the cell body of the output neuron, which fires whenever \hat{A} and \hat{B} are simultaneously active. In the first example, the output follows each discharge of the input except the first. In the second example, illustrating an effect analogous to anti-resonance, the output cell does not respond.

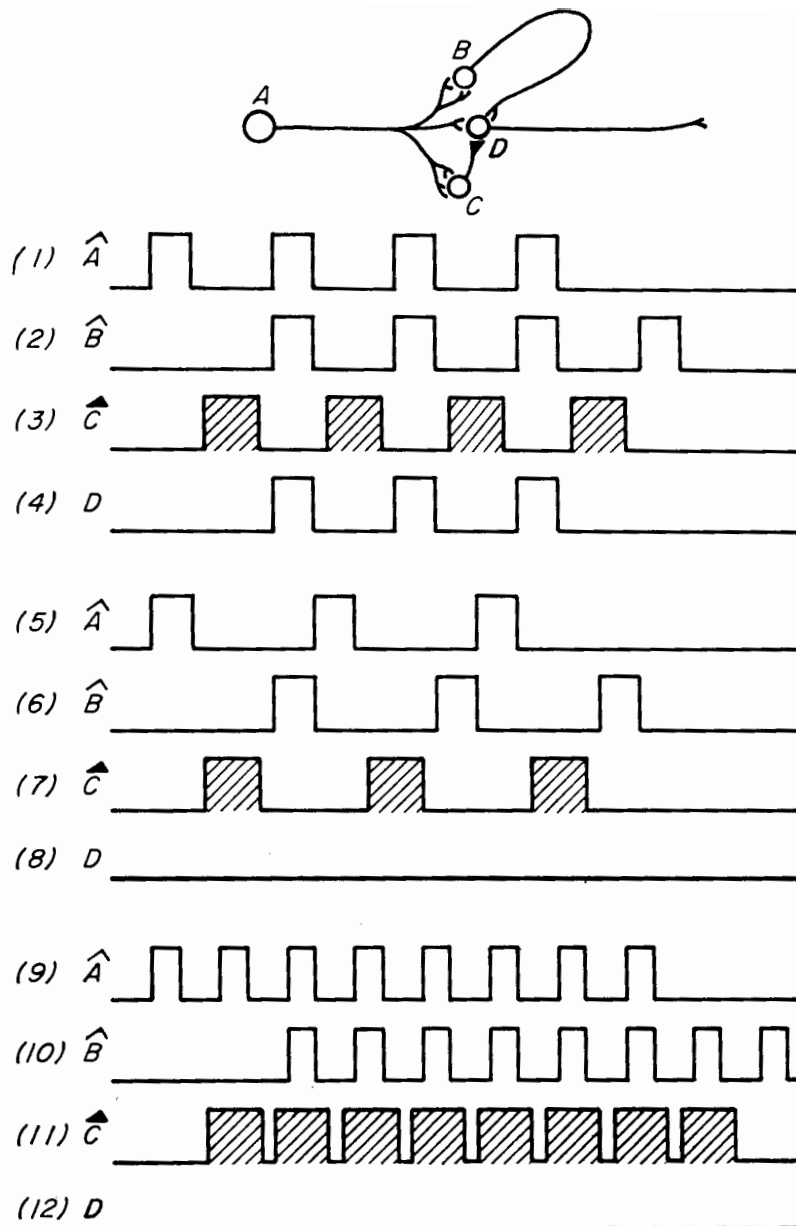


Fig. 3. Frequency-selective neuronal network employing inhibition. *D* is assumed to fire whenever \hat{A} and \hat{B} fire simultaneously and \hat{C} is inactive. The inhibitory effect of \hat{C} suppresses response to multiples of the input frequency in the illustration, but not to submultiples.

Perhaps the simplest schema for a neural filter is shown in Fig. 2. A is the input neuron. B is an auxiliary neuron, C is the output neuron. We must assume that, when A discharges, an excitatory signal appears at each of its three terminals, that the two excitations applied to B are sufficient to make B discharge, and that, whereas two would be sufficient, the one excitation at C is insufficient to make C discharge. Let the delay introduced by B be τ . Then, if the period of the input pulse train (1) is approximately equal to τ , the spatial summation effect at C gives rise to an output pulse for each input pulse except the first. However, if the input train is not „in tune” with a natural resonance of the filter, the output is zero. Note that this filter has more than one „resonance” — it is more like a comb filter than like a band-pass filter.

In the foregoing oversimplification, nothing was said about post-discharge refractoriness of the neurons, and no use was made of inhibition. Somewhat more complex arrangements of schematic neurons with those properties are capable of responding only to one band of input frequencies, of displaying build-up transients, of „ringing”, etc. The arrangement used in Fig. 3, for example, uses an inhibitory connection (blackened-in terminal) to suppress response to high-frequency input trains. The arrangement of Fig. 4, which doubtless would receive a low score if judged for cytoarchitectonic plausibility, illustrates the synthesis of a filter with an „impulse response” more nearly similar to the impulse response of a laboratory band-pass filter. All the synapses at B and C are assumed to produce faithful following of excitation. The terminals impinging upon D, on the other hand, contribute excitatory (B) and inhibitory (C) influences, and D responds if their sum is higher than some threshold value. The arrangement is therefore very sensitive to stimulation by pulses arriving at intervals near T , and therefore to pulse frequencies near $F = 1/T$. Although it might do so, it seems doubtful that the nervous system would need to go this far in approximation of laboratory filter characteristics.

It is easy to imagine a neural filter bank consisting of many filters more-or-less similar to the ones illustrated. If they were located in a wedge-shaped region of neural tissue, it might not be unreasonable to suppose that the filters at the apex of the wedge, restricted by geometry to have only short auxiliary neurons, might respond preferentially to high frequencies, whereas those near the base of the wedge, equipped perhaps with multi-neuron feedback chains, might respond preferentially to low frequencies. The notion of an array of filters thus seems to me worth holding in mind as a heuristic model — worth holding along with other notions, of course — for reference during efforts to „break” the code of the nervous system. One might be alert, for example, for any evidence of progressive changes in fiber lengths (or, better, in numbers of neurons in intercalated chains), and particularly for arrays more-or-less at right angles to the dimension of the tissue in which the cochlear frequency analysis is represented tonotopically. At the same time, he should keep in mind that neuronal arrangements at first glance dissimilar to those of Figs. 2 and 3 may be functionally equivalent. The arrangement of Fig. 5 (top), for example, is functionally equivalent (except for over-all time delay) to the arrangement of Fig. 2.

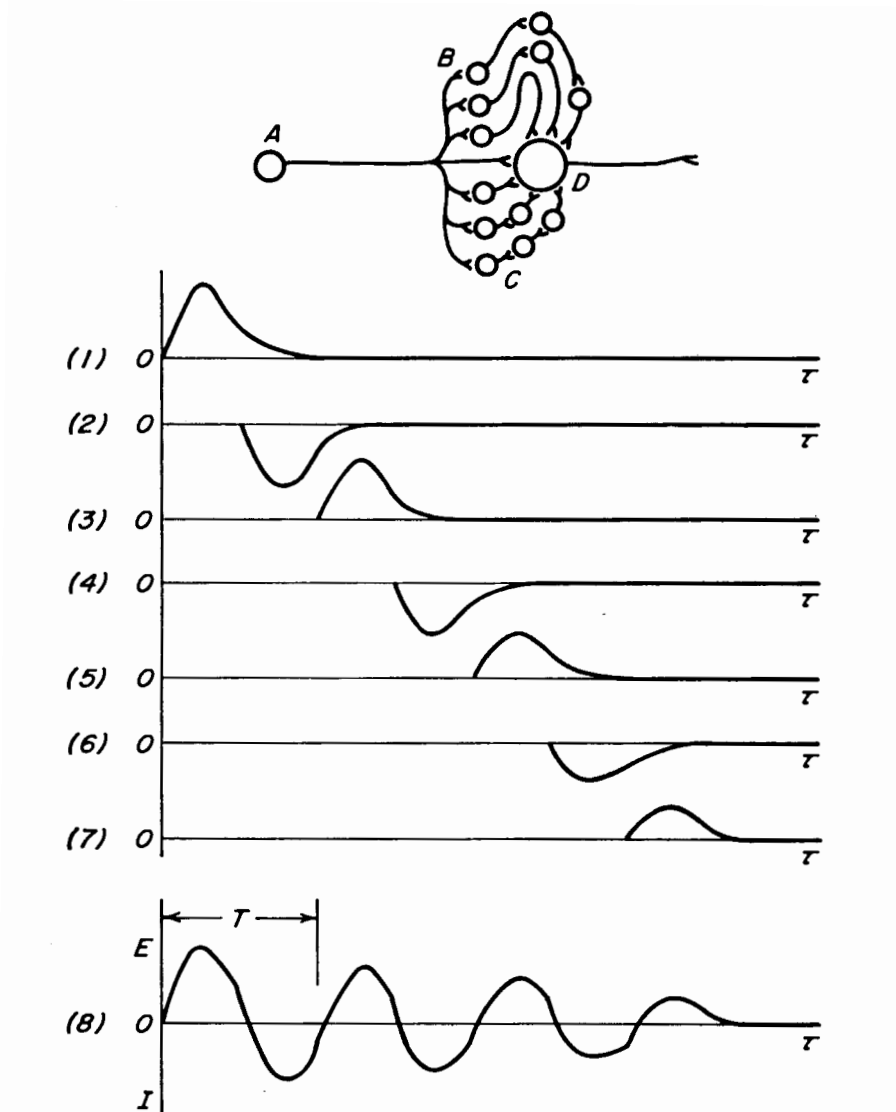


Fig. 4. Frequency-selective neuronal network showing a closer approach than Figs. 2 and 3 to the behavior of a familiar bandpass filter. The graphs show the excitatory processes set up individually (1—7) and collectively (8) by the auxiliary neurons in response to a single input impulse. The analogy between the collective curve of excitation versus time and the impulse response of a linear network is limited, but nonetheless suggestive of kinship between possible neural processes and filtering.

It is difficult for me to decide whether notions such as those illustrated in Figs. 2, 3 and 5 are ridiculously far-fetched or eminently reasonable. When I am inclined toward the former opinion, I may happen upon a schematic diagram of the lower part of the auditory nervous system or a histological plate showing the cochlear nucleus. Then I must ask myself whether the early division (in the cochlear nucleus) of the auditory system into two separate ascending branches (with preservation of tonotopic localization in both) and the later reconvergence (e.g., at the inferior colliculus) have a purpose, and whether the gross resemblance to Fig. 4 (bottom) is entirely coincidental.

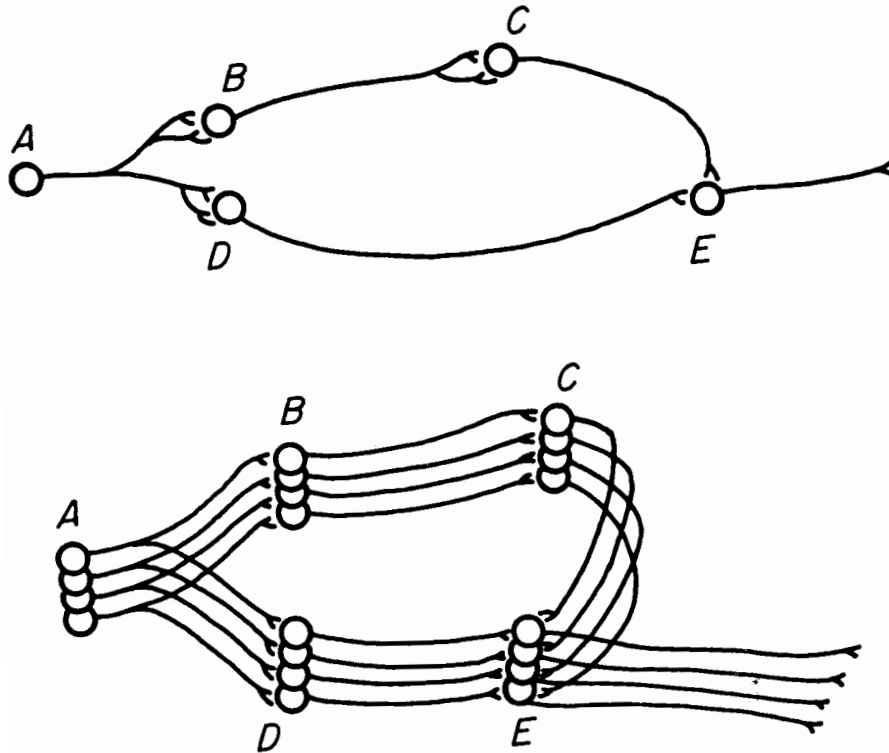


Fig. 5. Another frequency-selective neuronal network functionally equivalent to the network of Fig. 2. A single unit is shown at A; an array is shown at B. The essential characteristic is that the two paths have different time delays. This characteristic is basic, also, to the autocorrelator shown in Fig. 7.

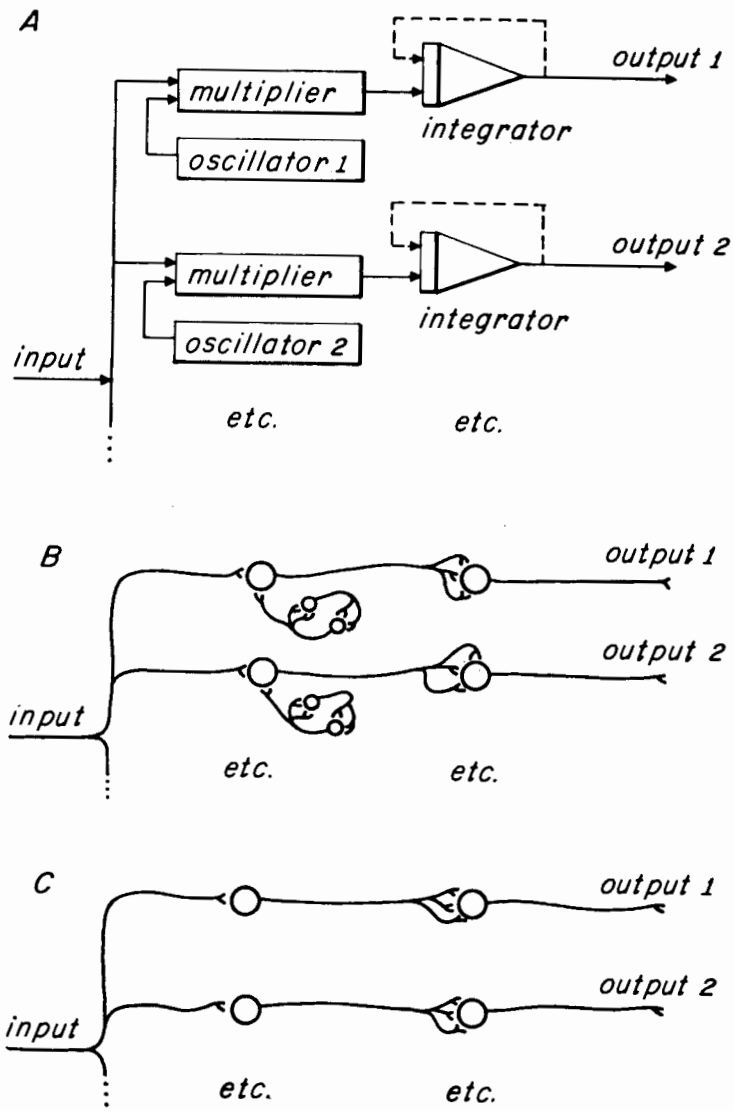


Fig. 6. Fourier transformers consisting of correlators fed by oscillators. A shows schematically an array in which an input waveform is multiplied by each one of several reference oscillations, after which each product is smoothed (by an integrator with negative feedback) to yield a running spectral coefficient. B and C illustrate neuronal approximations to A. In B, the reference oscillations are supplied by a recurrent circuit of neurons. In C, it is assumed that the first neuron in pair fluctuates periodically in sensitivity.

Fourier-Analyzer Model

Another way to effect periodicity-to-place transformations of essentially the kind produced by filter banks is to employ an array of correlators fed by oscillatory reference signals. Each element of the array must have a reference signal source, a multiplier, and an integrator (see Fig 6A). For our purpose, which is to make a short-time, running correlation, the integrator should be „leaky”. (The dotted lines in Fig. 6A convert the integrators of that figure into smoothing filters.)

Smoothing is accomplished, in the nervous system, by „temporal summation” at synapses. Multiplication is approximated by a scheme involving „spatial summation” (27). Periodic pulse trains may be generated by rings of neurons. A neuronal network to produce an approximate running Fourier transformation might therefore resemble Fig. 6B. The input signal is „multiplied” by a reference signal at the first cell body of each „correlator”, and the product is smoothed by the excitation process at the second cell body. The region of the second synapse might better be represented as a very complex meshwork of dendrites and/or small cells in order to suggest a smoothing time constant of perhaps 25 or 50 milliseconds.

It is well known that some neurons are „spontaneously” active and that others, without evident external influence, fluctuate periodically in sensitivity. A neuronal Fourier transformer might therefore appear macroscopically to be even simpler than Fig. 6B. In Fig. 6C, it is necessary to assume only that the first neuron in each horizontal line undergoes periodic fluctuations of threshold and that the second has a long period of temporal summation. The arrangement of Fig. 6C is then functionally equivalent to the arrangements of Fig. 6A and Fig. 6B.

Autocorrelator Model

Whereas the filter-bank and Fourier-analyzer models have not, to my knowledge, been proposed as definite auditory hypotheses, a scheme based on autocorrelational analysis has been described as a possible periodicity-to-place transformer (26, 27, 28). A single hypothetical autocorrelator is shown schematically in Fig. 7.

The purpose of an autocorrelator of the type illustrated is to determine, not a single coefficient, but a function. The function itself may progress with time: it is a running autocorrelation function. It carries the same information about the input waveform as does the running power spectrum — it represents everything except those features of the fine time structure that depend upon phase relations among frequency components that are not close neighbors to one another. The running autocorrelation function is

$$\varphi(\tau, t) = \overline{f(t) f(t-\tau)}$$

where $f(t)$ is the input waveform, τ is a variable shift in time, and the overbar designates the taking of a running average. In a neural autocorrelator, the time shift τ would be introduced by transmission of the signal through neural tissue, and it would appear in the output as a shift along a spatial dimension, say y . (A more detailed discussion of autocorrelation is given in reference 26.)

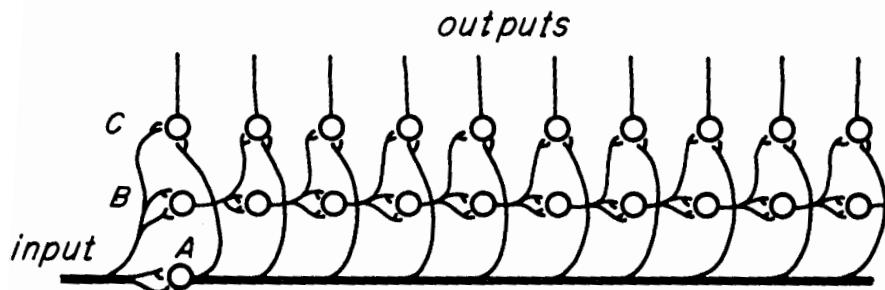


Fig. 7. Neuronal autocorrelator. The chain (B) of short neurons (or some other neural mechanism providing slow propagation) delivers the input signal to B synapses under increasing time delays, whereas the straight-through neuron (A) delivers it without significant delay. Spatial summation at B constitutes an approximation to multiplication. Temporal summation at C constitutes an approximation to smoothing. Thus the network produces an array of slowly varying output time functions that approximate the running autocorrelation function of the input time function.

The autocorrelational periodicity-to-place transformer involves an array of autocorrelators of the type illustrated in Fig. 7 and thus far discussed. It assumes that the signals in the various frequency channels of the afferent auditory pathway — the channels (along what we shall call the x dimension) that project the cochlear analysis upward — are fed to individual autocorrelators, and that each autocorrelator analyzes the periodicity of neural discharge in its particular channel. Each individual autocorrelator converts a single time function into a function of one spatial variable (the y dimension of the neural tissue) and of time. The array of autocorrelators therefore converts the array of neural time functions (one for each frequency channel along x) into a two-dimensional (x, y) manifold of ascending signals, each signal being a function of (gross) time. The macroscopic geometry of this process is illustrated in Fig. 8.

The autocorrelator model provides a rationale for several psychophysical facts. It provides a mechanism for the residue phenomenon, the pitch of interrupted random noise, the consonance of octaves, thirds, fourths, etc., and even to some extent for certain characteristics of „absolute” pitch judgments. These congruences between model and observation have been described (26-28). It seems unwarranted to redescribe them here. It may be worth noting, however, that two psychoacoustic phenomena not heretofore discussed in connection with the autocorrelation model are consonant with it. First, the „sweep pitch” described by Thurlow and Small (43) appears to arise when, and only when, there is a swath of the autocorrelation surface with periodic ridges at those values of τ (or y) at which ridges appear in response to a sinusoidal tone of the same pitch as the sweep pitch. Second, the ambiguity of the pitch of the residue set up by certain pulse patterns in experiments by Flanagan and Guttman (11) is consistent with the fact that different swaths of the autocorrelation surface may at a given moment have periodic ridge patterns with different periods, patterns corresponding to different low-frequency tones.

The autocorrelator model makes assumptions about the functional and topological (and to a limited extent the metric) interrelations of neurons in the auditory system, and it implies predictions about recordable electrophysiological events. At some points, the model can be held up against histological and electrophysiological facts, but there is available, to the best of my knowledge, no crucial confrontation.

The branching and reconvergence of the ascending auditory pathways, mentioned in connection with the filter-bank model, provides a gross structure as suitable for an autocorrelator as for an array of filters. The range of latencies observed in electrical responses of cells in the medial geniculate body (10 to 125 milliseconds) (16, 17, 42) indicates that there is easily enough relative time delay in the auditory tract to meet the design requirements of an autocorrelator. The midbrain, thalamic, and cortical auditory centers abound in fine structure suitable for either model. However, I know of no sharply indicative neuroanatomical evidence, and am therefore left with the feeling that the anatomical assumptions of the autocorrelation model are merely plausible — neither rejected nor strongly supported.

The electrophysiological side of the picture is only a little more definite. All three classes of models that we have considered imply that there is a two-dimensional tonotopic projection into one or more of the higher auditory centers, and that, if the meaningful reference frame of that projection is simply

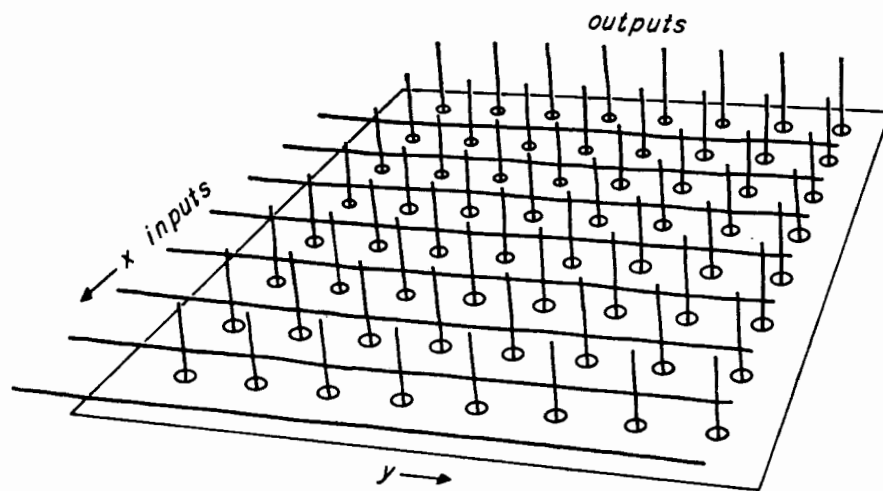


Fig. 8. Array of neuronal autocorrelators. Each horizontal subsystem corresponds to an autocorrelator of the type illustrated in Fig. 7. The array of autocorrelators performs a periodicity analysis upon the array of cochlear outputs, yielding a two-dimensional display of the activity that underlies subjective pitch.

a two-dimensional surface or two dimensions of a region of the neural tissue, responses to periodic high-frequency (residue-producing) signals should be recordable from somewhat different places than those responsive to aperiodic high-frequency (non-residue-producing) signals. Kiang and Goldstein (24) applied various periodic and aperiodic waveforms to the ear and recorded electrical potentials from strychninized spots on the auditory cortex of the anesthetized cat. They found no evidence at all of periodicity localization of the kind implied by the models. However, the cortex may not be the place to look for correlates of pitch, and the strychnine spike response (usually a transient response to transient stimulation) may not be the kind of indicator with which to search for a neural process underlying a sustained (pitch) experience. As Kiang and Goldstein say, the electrophysiological results do not argue for a pure place theory of pitch perception. The results seem to me to be slightly negative, but only a little below neutral, insofar as the periodicity-to-place conversion hypothesis is concerned.

Unordered-Array Models

Perhaps the least plausible assumption made in formulating the models thus far discussed is the assumption of ordering in the arrays of filters, oscillators, and delay channels. In proposing the autocorrelator model in the „duplex theory”, I stressed that the orderliness and regularity of arrangement shown in the schematic representations were introduced only for the sake of conceptual simplicity and might not be found in the nervous system (26). In discussing the „triplex” version of the theory (an extension designed to account for the Huggins-Cramer phenomenon), I noted that a random neuronal network would perform many of the operations performed by the deliberately organized networks (28). Here let us examine the implications of removing entirely the assumption of ordering in the arrangement of the arrays involved in periodicity-to-pitch conversion. (The order of elements in the x dimension, arising from the cochlear frequency analysis, is of course retained.) The assumptions involved in the three classes of models are reduced, by this elimination, to specifications that there exist, in the neural tissue corresponding to each interval along the x dimension, several of the following:

1. delay elements capable of introducing assorted values of τ ;
2. coincidence-sensitive synapses;
3. synapses or networks capable of temporal summation;
4. recurrent neuronal circuits or other devices capable of producing more-or-less sustained oscillation;
5. inhibitory as well as excitatory influences; and
6. spontaneous periodic fluctuation of sensitivity.

Those assumptions correspond to standard, or at least to demonstrated, characteristics of the behavior of central neurons, synapses, and nets. It seems very unlikely, therefore, that a haphazard network of many thousand neurons would fail to approximate, in one small zone or another, filtering **and** correlation with a reference oscillation **and** correlation with the delayed input signal, itself. Given tens or hundreds of thousands of neurons in quasi-random configuration, one might find band-pass filtering approximated with

several different center frequencies and bandwidths, correlation approximated with several reference-oscillation frequencies and smoothing time-constants, etc. If the ordering of arrays is not crucial, that is to say, one might argue that the auditory nervous system can hardly avoid incorporating all three kinds of model, and other permutations of the basic operations as well.

Of what consequence to the nervous system, then, would be the ordering of similar component processes into graded sequences following spatial dimensions in the tissue? Why would a designer **introduce** such ordering? If it came as a by-product of some other effort, if it were simply easier to build an ordered frequency analyzer (e.g., a cochlea) than a haphazard one, then well enough — but is there any intrinsic advantage in achieving the order of the graded sequence that should lead one to postulate such order in a model of the kind with which we are here concerned?

It seems to me that a fundamental place principle of neural processing is **collocation for correlation**: bringing together in one place those subprocesses that must be interrelated and integrated to represent a unitary concept or object or to carry out a coherent act. If the main business of evolving organisms had been to serve as subjects in experiments on the missing fundamental, then, according to the principle, periodicity pitches would be lined up next to one another, in regular ascending order, as suggested by the diagrams of models. On the other hand, if the main business involved the identification of diverse objects partly on the basis of their sounds, then the pitches made by particular objects or classes of objects would be separated from other pitches and coupled closely to characteristic timbres and volumes and shapes and textures. This line of thinking leads me to devalue (though not entirely) the hypothesis that there is order in what we have been referring to as the y dimension. Order and sequence are present at the outset in the x dimension, thanks to the cochlear analysis. It seems likely, however, that nature probably leaves the y dimension in disorder — that the preferred model for the untrained organism is a model involving periodicity-to-place conversions that assign the various periodicity pitches to more-or-less randomly selected places in a nucleus of the auditory system. Nature, then, may shape up whatever arrangements and organizations are required to meet the demands of individual experience.

A discussion of the „triplex theory“ contains some speculations about a process through which an organized network might be developed by training and experience (28). However, I think much experimentation with simulated neuronal networks will be required to develop an understanding of such a process. Let me therefore go no further on that path now.

Property Filters

The idea that elementary processing operations may be arranged in quasi-random and therefore diverse configurations in the auditory system tends to open the domain of speculation beyond frequency and periodicity analyzers. One envisions an aggregation of processing units — filters in a very generalized sense — each one selectively responsive to one or more spatio-temporal patterns of incident excitation. Some of these units might approximate

paradigms of the type we have discussed and respond selectively to particular frequencies. Others might respond selectively to particular distributions in the x dimension of their milieu, and thus to particular acoustic energy spectra. Still others might respond to particular binaural coincidences (see below) or to excitation patterns set up by clicks, trills, glissandi, etc. Each unit would „recognize” the presence of a particular property in the neural excitation reaching it — which is almost to say, a particular property of the stimulus.

Galambos (15) has described electrophysiological observations that indicate that some neurons in the auditory cortex (and some in the medial geniculate body) of the cat do behave in the way just described. Mountcastle (30) has found property filters in the spinal somesthetic system of the cat. Letvin et al. (25) have found them in the optic nerve of the frog. Evidently, property filters are fundamental building blocks of neural processes. In research in the new field of „artificial intelligence”, property lists are among the most sophisticated techniques of pattern recognition, and property filters are employed in several of the most successful pattern-recognition systems (29). Under the influence of these considerations, I find myself tending to recast hypothetical auditory mechanisms in such a way as to emphasize the kinds of analysis that lead to synthesis (pattern recognition, object construction, concept formation, problem solving) as opposed to the kinds of analysis that lead to scales that correspond to sensory attributes. This tendency does not deny the scalability of sensory attributes, nor the primary nature of such attributes as the one based upon the cochlear frequency analysis. It does, however, de-emphasize the need for ordered sequences, and it emphasizes the importance of variety in the arrangement of the elements of neural processing systems.

SHARPENING, FUNNELING, SEPARATION AND FUSION, AND BINAURAL INTERACTION

Models designed to account for periodicity pitch should be consistent with models designed to account for other major auditory phenomena. Ideally, models of various subordinate processes should fit together into one coherent theory of hearing. Although it is not possible to advance very far toward that ideal with the parts presently available, something should be said about some of the other processes that are closely associated with the hypothetical processes underlying the periodicity-to-place transformation.

Sharpening

As mentioned earlier, the cochlear frequency analysis is not very sharp. Much of the basilar membrane is set into vibration even by pure-tone stimulation. Successive stages of the auditory process, all the way up to the medial geniculate body, concern themselves, in part at least, with the task of sharpening further the distributions of activity that ascend the auditory pathways in response to frequency-structured sounds (16, 42). Is the fine time pattern of the neural signals involved in the sharpening process?

Periodicity analysis of the general type we have been discussing serves some of the same purposes as sharpening of the peaks in the x distribution of neural activity. Periodicity pitch extracts important information from that part of the spectrum in which the cochlear frequency analysis is least sharp. It displays that information in a convenient way, one that changes progressively, as the period increases, from a continuous pitchlike quality through gradations of increasing roughness until, as the analysis breaks down, the sound becomes sensibly intermittent and the stimulus time structure is perceived as a succession of events in phenomenal time. This way of handling fine temporal detail seems preferable to straightforward augmentation of resolution in frequency, which would be difficult to blend into perception of gross time.

There appears to be no clear evidence that the fine time or frequency structure of the neural signals plays any role, beyond that associated with periodicity pitch, in the sharpening process. In a paper on place mechanisms of frequency analysis, Huggins and I (22) once said that we planned a sequel on time-domain mechanisms; the sequel did not materialize, mainly for want of ideas beyond those relating to periodicity pitch.

Hypothetical place mechanisms of sharpening depend mainly upon (1) special lateral extensions or courings of sensory neurons, (2) lateral interconnections in central nerve nets, or (3) simultaneous convergence and divergence in projection systems. One of the basic principles is that focused, sharply localized excitatory influences combined with diffuse, spreading inhibitory influences, produce sharpening of peaks and contours (22). There is no evident incompatibility between arrangements of the kind required for sharpening and those hypothesized for periodicity-to-pitch conversion. The main obstacle to bringing the two kinds of paradigm together in one model is that it is very difficult to incorporate so much detail into a comprehensible verbal and pictorial description. The main hope appears to lie in simulation through digital computer programs.

Funneling

Békésy (4-6) has defined and used repeatedly a principle related to sharpening but incorporating an additional feature. It is convenient to describe it by referring to a somesthetic phenomenon that he observed (4). When force is applied steadily to a long, narrow area of his skin, it gives rise for a prolonged period to a correspondingly long, narrow image. When, however, the force is applied suddenly, it feels as though the blow were confined to a short segment near the middle of the stimulated strip — but the overall strength of the sensation is not correspondingly diminished. It is as though all the stimulus energy were poured through a sensory funnel into the short, central segment.

There appear to be two main approaches toward development of a model of the underlying process. The term „funneling” is more appropriate to the first than to the second.

(1) In keeping with the basic idea of funneling, one might devise a neuronal network in which peripheral parts of an ascending (or in-flowing) pattern

of neural activity progressively decline in strength, while central parts increase in strength. The lateral extent of the pattern would decrease, but the total amount of activity would remain approximately constant. Such a mechanism can be constructed with schematized neurons having excitatory and inhibitory interconnections.

(2) In keeping with the idea of property filters, on the other hand, one might set up an arrangement in which various neural units measure (respond selectively to) diverse aspects of the peripheral excitation pattern: its strengths in various parts of the area, its gradients, its curvatures, etc. Other neural units, perhaps at a higher level, would respond to signals from combinations of peripheral units. The responses of some of the latter would be diagnostic with respect to „where”, others to „how much”, still others to „what shape”, etc. The perceptual mechanism would then synthesize a sensation by using the diagnostic responses as data for a decision process. In such a model, the gross pattern of neural activity might or might not actually converge as though funneled, and the total amount of activity might remain constant, decrease, or increase. As soon as the information is encoded (presumably in the „place” of the measuring unit or property filter), the amount of activity becomes less important as a variable.

It is necessary, of course, to design into the second type of model, just as into the first, the basis for the „mistake” in the judgment of the spatial distribution of the sudden blow. However, the necessary features could be designed into the extent-measuring part of the system without having to affect materially the parts responsible for determining such other characteristics as the center coordinates and the total force of the blow.

The foregoing considerations apply also, of course, to hearing. The second approach is highly compatible with the unordered periodicity-to-place models. It leads one to think of measuring separately the pitches and loudnesses of the several parts of a compound signal, and then synthesizing the sensation from the measured data.

Separation and Fusion

What are the „parts” of a compound signal? How are the superposed sounds of several voices or instruments, for example, separated in analysis and assigned individual pitches, timbres, loudness, etc.? Or, to look at the opposite face of the coin, how can certain parts of a spectrum be brought together to form one unitary sound, while other parts form a second unitary sound, and still other parts make up a distributed noise? As Sayre and Cherry (33) have emphasized, the problem of separation and fusion is fundamental. It is fundamental to pitch perception, because the several parts of a compound auditory sensation may have distinct pitches. It is fundamental to binaural hearing, because approximately paired parts of a dichotic signal fuse together while other parts fail to fuse and are localized separately near the listener's ears.

It is beyond the scope of this paper to attempt to examine fusion hypotheses exhaustively. Let us limit ourselves, therefore, to a few ideas concerning fusion that have been related also to periodicity pitch.

Binaural Interaction

In trying to extend the „duplex theory” (autocorrelator model) in such a way as to account for the Huggins-Cramer phenomenon, I borrowed a notion from Wallach (44) and Jeffress (23) that can be called, with some appropriateness, a cross-correlator model. I shall not describe its action here. The presently relevant point is that it seemed necessary to have the mechanism of binaural interaction (i.e., the cross-correlator) operate rather directly upon the cochlear output in order, for example, to separate the homophasic from the heterophasic parts of the Huggins-Cramer noise and at the same time fuse the left and right homophasic parts into one unit and the left and right heterophasic parts into another unit. The cross-correlator was assigned a short smoothing time-constant, and its output could be used as the input signal for the periodicity-to-place mechanism (the autocorrelator). If the autocorrelator, which had to have a longer time-constant, had been placed first in a tandem configuration, the cross-correlator would not have had a reasonable input signal.

As I see it now, it would have been better to adopt the property-filter approach, to have regarded the periodicity measurements and the interaural-time-delay measurements as measurements of separate properties that could just as well be determined in parallel. The periodicity-to-place transformation mechanism should probably be associated with an extended segment of the afferent pathways, starting at the cochlear nucleus, whereas the binaural-interaction mechanism might well be associated with a part of one of the pathways that includes the olivary complex (18, 40). The binaural-interaction mechanism should of course be up-dated by talking into account, as Van Bergeijk (1) has done, the new anatomical and physiological information (18, 40) about the olivary body which reveals its accessory nucleus as a highly specialized arrangement obviously designed to handle interaural time delays. Neurons of the accessory nucleus have two dendrites, one reaching out toward the left ear and the other reaching out toward the right, and firing is inhibited by certain temporal relations between excitations applied by the two dendrites. The existence of this so specialized component in the auditory system lends support to the idea that, whereas the general features of auditory processing are similar to those of the skin senses (4-6), a considerable amount of **ad hoc** design is defensible in formulating models of auditory processes.

After modification to take into account the new information, the model for binaural interaction looks somewhat less like a cross-correlator than it did before, but it clearly behaves like a cross-correlator. That is evident in the results of Cherry and Sayres, who demonstrated remarkable correspondence between the responses of a cross-correlator model and the laterality judgments of subjects listening to a variety of dichotic sounds (7).

The property-filter approach (but not the notion of unordered arrays) appears to be applicable even to the aspect of pitch that is based on the cochlear analysis and represented in the x dimension of the tissue. With that approach, triplex theory could account for a theoretically crucial phenomenon observed by Franssen (14). Franssen listened to an ingeniously contrived

dichotic signal consisting of two pulses of oscillation. The pulse delivered to the left ear led in time and oscillated at frequency f_l , but it was short and (heard alone) almost devoid of pitch. The pulse delivered to the right ear, which followed in time, oscillated at frequency f_r , well separated from f_l , and it was long enough to have a definite pitch. When the two pulses were presented together, one to one ear and the other to the other, the listener heard a single, fused sound. It appeared to be located near his left ear, but its pitch corresponded to f_r . Evidently, the auditory system handled the questions of pitch and localization separately and made an „error” in the process of synthesizing a sensation to explain the data economically.

„PERIODICITY PITCH” ET MODELES ALLIES DE PROCEDES AUDITIFS

Le phénomène résidu de Schouten (34-38) contredit clairement la théorie de location (**place theory**) de la perception de la période subjective (**pitch**), car le résidu possède une période subjective qui n'est pas propre aux canaux de la fréquence Fourier du système auditif par laquelle elle est entendue. Quand, par exemple, un stimulant ondulatoire (voir Fig. 1A) (qui ne contient pas d'énergie à basse fréquence) se trouve en face d'un fond intense de bruit à basse fréquence, l'auditeur entend un ton bas (le résidu), bien qu'on puisse supposer que seuls sont activés les canaux inférieurs de haut fréquence du nerf auditif (27, 28). (Quand une sinusoïde à basse fréquence se trouve en présence du même bruit de fond, aucun son n'est entendu; le signal de basse fréquence est entièrement masqué par le bruit.) Evidemment quelque révision de la théorie de location pure est nécessaire pour cette raison.

La théorie de location est si efficace pour l'explication d'autres phénomènes auditifs et si bien en accord avec des observations neurophysiologiques, qu'on ne peut penser à la rejeter et à remplacer. Au lieu de cela il paraît approprié de l'étendre pour donner un mécanisme qui obéit la périodicité dans les décharges de neurones (ou de groupes de neurones) dans des centres bas du système auditif et qu'une telle périodicité est converti en location dans des centres plus hauts. Un tel mécanisme pourrait offrir une explication pour le résidu de période (**residue pitch**), la période subjective du bruit blanc interrompu, la consonance musicale, et d'autres phénomènes (26).

Il y a trois sortes de mécanisme général qui s'offrent pour étendre la théorie de location. Elles sont typifiées par 1.) le modèle des groupes de filtres (voir Figs. 2-5), 2.) le modèle de l'analyseur de Fourier (voir Fig. 6), et 3.) le modèle de l'autocorrélateur (voir Figs. 7 et 8). Il apparaît possible que le système nerveux, quand il emploie seulement les opérations établies et élémentaires du délai de temps, le sommation dans l'espace, la sommation dans le temps, **recurrent-circuit feedback**, l'excitation, et l'inhibition pour exécuter les fonctions qui se trouvent dans les trois modèles.

En pensant à des filtres des analyseurs de Fourier, ou des autocorrélateurs, on imagine probablement des rangées de composantes bien organisées. Naturellement, il est concevable que le système nerveux emploie, dans son analyse de périodicité secondaire, des rangées organisées, comme il le fait dans l'analyse primaire de fréquence de Fourier exécutée par le cochléa et accentuée par l'action des noyaux (**nuclei**) dans les chemins auditifs. Il est peut-être plus raisonnable, d'autre part, d'imaginer l'analyse hypothétique de périodicité secondaire comme la font les parties distribuées plus ou moins au hasard à travers le tissu, ou, en tout cas, pas alignées avec soin dans les séries graduées qui se trouvent le long d'un chemin défini dans le tissu. Considération du problème suggère que bien peu serait perdu en abandonnant l'ordre des séries graduées et que même une certaine flexibilité pourrait être gagnée. Il pourrait même être aussi important de rapprocher dans un seul voisinage tous les signaux nerveux qui normalement arrivent ensemble en présence d'un certain objet stimulant, que de ranger les diverses périodicités en ordre numérique le long d'un continuum nerveux.

Etant donné un substratum nerveux ayant initialement une forme de réseau presque au hasard, on peut s'attendre de trouver des arrangements locaux de nerfs qui agissent comme des filtres, d'autres comme des corrélateurs, et d'autres qui font d'autres opérations élémentaires que nous n'avons pas considérées ici. Ainsi les configurations locales peuvent être considérées comme différents „réseaux de mesure" chacun ayant sa mesure particulière à prendre à son entrée (**input**), soi-disant „filtres de propriété" (**property filters**), chacun ayant sa propriété particulière à abstraire si cette propriété se trouve à l'entrée (25, 30).

La tendance présente est de penser en termes semblables à ceux de la transformation de périodicité en location. Ils sont compatibles avec les idées de procédés en parallèle, et de l'organisation propre par expérience, et ils permettent à la transformation périodicité-location de se trouver dans les mêmes parties générales du système auditif qui sont responsables de l'aiguillage de l'analyse de fréquence du cochléa et de l'action de localisation du son.

J. C. R. Licklider,
Bolt, Beranek and Newman Inc.,
50 Moulton Avenue,
Cambridge, U.S.A.

1. W. A. van Bergeijk, Mimeographed paper, undated; received 21 May 1962.
2. G. v. Békésy, J. Acoustical Soc. Am. 19, 452, 1947.
3. G. v. Békésy, J. Acoustical Soc. Am. 21, 233, 1949.
4. G. v. Békésy, J. Acoustical Soc. Am. 29, 1059, 1957.
5. G. v. Békésy, J. Acoustical Soc. Am. 33, 341, 1961.
6. G. v. Békésy, J. Acoustical Soc. Am. 33, 888, 1961.
7. E. C. Cherry and B. McA. Sayers, J. Acoustical Soc. Am. 28, 889, 1956.
8. E. M. Cramer and W. H. Huggins, J. Acoustical Soc. Am. 30, 413, 1958.
9. J. L. Flanagan, Bell Syst. Tech. J. 39, 1163, 1960.
10. J. L. Flanagan, J. Acoustical Soc. Am. 34, 1962.
11. J. L. Flanagan and N. Guttman, J. Acoustical Soc. Am. 32, 1319, 1960.
12. H. Fletcher, Phys. Rev. 23, 427, 1924.

13. H. Fletcher, *Speech and Hearing in Communication*. New York: Van Nostrand 1953.
14. N. V. Franssen, *Some Considerations on the Mechanism of Directional Hearing*. Doctoral dissertation, University of Delft, 1960.
15. R. Galambos, *Laryngoscope* 68, 388, 1958.
16. R. Galambos and J. E. Rose, *J. Neurophysiol.* 15, 381, 1952.
17. R. Galambos, J. E. Rose, R. G. Bromiley, and J. R. Hughes, *J. Neurophysiol.* 15, 359, 1952.
18. R. Galambos, J. Schwartzkopff, and A. Rupert, *Am. J. Physiol.* 197, 527, 1959.
19. M. H. Goldstein Jr., and N. Y-S. Kiang, *J. Acoustical Soc. Am.* 30, 107, 1958.
20. H. L. F. Helmholtz, *Sensations of Tone*. A. J. Ellis, trans. New York: Longmans, Green and Company, 1930.
21. G. A. Hoogland, *The Missing Fundamental*. Doctoral dissertation, University of Utrecht, Utrecht, The Netherlands: Drukkerij Fa. Schotanus en Jens, 1953.
22. W. H. Huggins and J. C. R. Licklider, *J. Acoustical Soc. Am.* 23, 290, 1951.
23. L. A. Jeffress, *J. Comp. Physiol. Psychol.* 41, 35, 1948.
24. N. Y-S. Kiang and M. H. Goldstein, jr., *J. Acoustical Soc. Am.* 31, 786, 1959.
25. J. Y. Lettvin, H. R. Maturana, W. H. Pitts, and W. S. McCulloch, *Two Remarks on the Visual System of the Frog*. Chapter 38 in W. A. Rosenblith, ed., *Sensory Communication*. Cambridge, Massachusetts: M.I.T. Press, 1961.
26. J. C. R. Licklider, *Experientia* 7, 128, 1951.
27. J. C. R. Licklider, *Auditory Frequency Analysis*, In C. Cherry, ed., *Information Theory*. New York: Academic Press, 1956.
28. J. C. R. Licklider, *Three Auditory Theories*. Chapter in S. Koch, ed., *Psychology: A Study of a Science*. New York: McGraw-Hill Book Co., 1959.
29. M. Minsky, *Proc. Inst. Radio Engrs.* 49, 8, 1961.
30. V. B. Mountcastle, *Some Functional Properties of the Somatic Afferent System*. Chapter 22 in W. A. Rosenblith, ed., *Sensory Communication*. Cambridge, Massachusetts: M.I.T. Press, 1961.
31. G. S. Ohm, *Ann. Physik. Chem. (Pogg. Ann.)* 59, 513, 1843.
32. G. S. Ohm, *Ann. Physik. Chem. (Pogg. Ann.)* 62, 1, 1844.
33. B. McA. Sayers and C. Cherry, *J. Acoustical Soc. Am.* 29, 973, 1957.
34. J. F. Schouten, *Proc. Konink. Nederlandsche Akad. Wetenschappen* 41, 1086, 1938.
35. J. F. Schouten, *Philips Tech. Rev.* 4, 167, 1939.
36. J. F. Schouten, *Philips Tech. Rev.* 5, 286, 1940.
37. J. F. Schouten, *Proc. Konink. Nederlandsche Akad. Wetenschappen* 43, 356, 1940.
38. J. F. Schouten, *Proc. Konink. Nederlandsche Akad. Wetenschappen* 43, 991, 1940.
39. A. Seebeck, *Ann. Physik. Chem. (Pogg. Ann.)* 53, 417, 1841.
40. W. A. Stotler, *J. Comp. Neurol.* 98, 401, 1953.
41. I. Tasaki, *Ann. Rev. Physiol.* 19, 417, 1957.
42. I. Tasaki, E. H. Polley, and F. Orrego, *J. Neurophysiol.* 17, 454, 1954.
43. W. R. Thurlow and A. M. Small, Jr., *J. Acoustical Soc. Am.* 27, 132, 1955.
44. W. Wallach, *Personal Communication*, 1942.
45. E. G. Wever, *Theory of Hearing*. New York: John Wiley and Sons, Inc., 1949.