

Pitch Perception [version 090507]

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1 Introduction

Pitch is the stuff of which music is made. Melody, harmony, tonality are either built upon pitch, or else they depend upon similar properties of the physical stimulus. In speech, pitch is a vector of prosody, and for tonal languages it carries also syllabic information. Pitch (or its physical correlate, periodicity) is important to perceptually segregate competing sound sources. Pitch and harmony have fascinated thinkers since antiquity and, for many early authors, to explain pitch amounted to explaining auditory perception.

For the psychoacoustician, pitch is the perceptual correlate of fundamental frequency (**F0**), that is, the rate at which a periodic waveform repeats itself. A periodic sound produces a pitch that depends on the period $T=1/F0$: the shorter the period, the higher the pitch. The quantitative relation between period of vibration and notes of the musical scale was established early in the 17th century by Mersenne and Galileo (see de Cheveigné 2005 for a review). Recent work has been invested in mapping out the properties and limits of pitch perception (Plack and Oxenham 2005), and probing the mechanisms by which the pitch percept emerges within the auditory system (Winter 2005).

Stimuli may differ in amplitude, duration, spatial position, and spectral content, and nevertheless evoke the same pitch. Pitch is a many-to-one mapping from a high dimensional set of sounds to a percept that is unidimensional (in first approximation). Thus, a trained listener may accurately match a piano note to a pure tone, to a complex tone with high-order partials, or to an exotic binaural stimulus that sounds like a featureless "shhhh" when listened to with one ear, but is distinctly pitch-like when listening with both ears (Cramer and Huggins 1958). Pitch is the abstract quality common to these sounds. To understand pitch perception, we must explain not only our exquisite sensitivity to small changes along the physical dimension of period (or fundamental frequency), but also our ability to ignore enormous differences along other dimensions.

It is customary in psychoacoustics to distinguish *pure tones*, with a sinusoidal waveform and a single-component spectrum, from *complex tones* with a waveform that is arbitrarily shaped but nevertheless periodic, and a spectrum with multiple components that are harmonically related (i.e. all multiples of the same **F0**). Much past research on pitch has focused on pure tones under the belief that the percept that they evoke is somehow

"elementary". Here we treat the pure tone as one among the many stimuli that may evoke a pitch. Some examples of pitch-evoking stimuli are illustrated in Fig. 1.

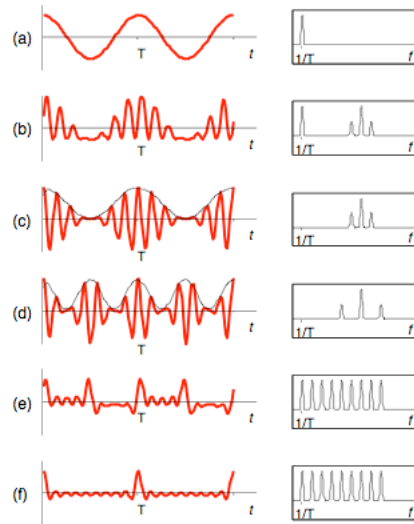


Fig. 1. Waveforms and spectra of various stimuli that evoke pitch. Stimuli with the same period tend to evoke the same pitch despite their different amplitude, duration, spectra, or spatial characteristics. (a) Pure tone, (b) Complex tone made up of the fundamental and three higher harmonics. (c) Same, without the fundamental. (d) Same, with partials spaced by twice the F_0 . (e) Complex made up of 9 partials in alternating sine/cosine phase, (f) Same, in cosine phase. The stimuli in (c) and (d) can be described as the result of modulating a carrier of frequency $f=7/T$ by a more slowly-varying *temporal envelope* (thin line). The frequency of the temporal envelope is equal to the spacing of the partials, whereas the fundamental frequency $F_0=1/T$ is equal to the largest common divisor of the partial frequencies. For some stimuli, pitch may follow the period of the temporal envelope, rather than the true fundamental, i.e. tones as in (d) (and also e) may sound an octave higher than expected based on their F_0 . In the spectral domain, the *spectral envelope* is a smooth function of frequency that describes the amplitude of the partials. The spectral envelope determines mainly the timbre.

2 What is pitch?

In 1960 the American Standards Association defined pitch as "that attribute of auditory sensation in terms of which sounds may be ordered on a musical scale" (ASA 1960), a definition that suggests a percept with extent along a linear perceptual dimension. The concept of "dimension" carries the idea that diverse sounds may map to the same point along this dimension. Indeed, notes produced on different instruments may have distinct timbres

but the same pitch. A more recent version of the standard (ANSI 1994) added that pitches are ordered from *low to high*, suggesting a vertical orientation for this dimension. Whether this orientation is universal or cultural is a matter of debate (e.g. Rusconi et al. 2006), but in our culture it fits the vertical axis of a musical score or a spectrogram.

In music, pitch usually varies over time. Every new note of a melody evokes a percept that depends to some extent on the physical characteristics of that note, but also on the note that precedes it. Indeed it may seem that our perception of melodic pitch is determined by *intervals* between notes rather than, or in addition to, the notes themselves. More generally, the musical effect of each new note depends strongly on its context (Bigand and Tillmann 2005), a property that is not quite captured by the ANSI definitions, or indeed, by most psychoacoustic accounts of pitch.

To a first approximation, equal *ratios* of frequency produce pitch steps of equal salience, as if pitch were a logarithmic function of frequency. However, the relation between notes on the scale is also governed by complex rules of harmony, also not captured by the standard definition of pitch. For example, notes an octave apart are perceptually similar, and in some cases interchangeable. They are said to share the same *chroma*. Chroma is an equivalence relation: multiple notes map to the same chroma. The similarity between two notes depends in part on their proximity along a logarithmic frequency scale, and in part on their chroma.

To capture this property, more complex geometrical models of pitch have been proposed, such as a helix with a linear axis that fits the standard "low-to-high" dimension of pitch height, and a circular dimension of chroma (Giangrande et al 2003; Bachem 1950; Ueda and Ohgushi 1987). Yet more complex structures such as toroids have been proposed to incorporate additional tonal relations such as fifths (Shepard 1982). However it has been argued that they may reflect less the perceptual structure of pitch than the harmonic spectra of most European instrumental sounds (Sethares 1987; Burns 1981). In any case, the fixed nodes of such a structure cannot capture dynamic effects noted earlier, such as determined by the order in which two notes appear (Giangrande et al 2003; Bigand and Tillmann 2005).

A fascinating aspect of pitch perception is inter-individual variability. Discrimination thresholds vary between individuals over several orders of magnitude. Thresholds improve considerably with training (Demany and Semal 2002; Micheyl et al 2006a), and thus experience may account for some differences between listeners. Genetic factors may also contribute (Drayna et al 2001; Douglas and Bilkey 2007), and there are hints that the phenomenology of pitch may actually differ among people. For example Semal and Demany (2006) found that most subjects can judge the direction of a pitch change (high to low or vice-versa) as soon as it is detectable, but other subjects found it impossible to say which note is higher, for a pitch difference that they nevertheless could detect with ease.

Absolute pitch is the relatively rare capability to assign labels to pitches regardless of context (Levitin and Rogers 2005; Ward 1999; Zatorre 2003; Hsieh and Saberi 2007). Most listeners possess instead *relative pitch*, the ability to judge the pitch of a note relative to a preceding note. This question is interesting because the two forms of pitch imply rather different mechanisms. For example most models of pitch easily account for absolute

pitch but not relative pitch. Something else is required for relative pitch, and as both types of pitch exist, the brain must be capable of both.

To summarize, pitch is a very important aspect of sound perception. We can discriminate exquisitely small differences in pitch, while ignoring salient differences along other perceptual dimensions. Pitch has more to it than the simple, one-dimensional construct assumed by psychophysics, and yet we have few models to account for these complexities. That so much is yet unknown about pitch is sobering for those of us who have been working on it for years, and exhilarating for whoever sets out to search for more: there's lots more to discover!

3 The limits of pitch

Periodic stimuli evoke pitch over a very wide range of their parameters: **F0**, amplitude, duration, spectral envelope, etc. Pitch is exquisitely sensitive to the first parameter (**F0**), and yet remarkably *stable* over large variations of the others, variations that themselves may produce salient changes in loudness, subjective duration, or timbre. Stimuli that are only approximately periodic may also evoke a pitch (inharmonic complexes, stimuli in noise), and the same may occur for stimuli that are, strictly speaking, not periodic at all, such as amplitude-modulated noise or binaurally correlated noise. Conversely a periodic stimulus may fail to evoke a pitch if its parameters fall outside certain bounds that delimit the *region of existence* of pitch.

Musical pitch arises if the **F0** is within a range of about 30 Hz to 5000 Hz. At the lower end of the scale, Pressnitzer et al. (2001) found that subjects failed to detect a one-semitone mistuning in a four-note chromatic melody if its lowest note fell below 30 Hz (33 ms). Periodicity can be detected, and the period discriminated, for longer periods up to several seconds but the percept is not "musical", and discrimination thresholds are large (Warren et al. 1980; Kaernbach 1993). Thresholds improve by an order of magnitude as **F0** increases from 16 Hz to 64 Hz (Krumbholz et al. 2000). At the other end of the scale, stimuli lose their musical properties beyond about 5 kHz (Semal and Demany 1990; Bachem 1948). The limit is rather sharp (subjects report a "highest musical note") but it is subject- (and even ear-) dependent. Burns (1983) nevertheless found that some subjects performed above chance on musical tasks at frequencies of 10 kHz or beyond.

Difference limens for pure tones (expressed as a proportional change in frequency) are smallest at around 1-2 kHz (about 0.2% for good subjects) but they increase abruptly as frequency exceeds 4 kHz (Moore 1973) (Fig. 2). The interval from 30 Hz to 4000 Hz spans about seven octaves and includes the range of most musical instruments.

Pitch changes remarkably little with level. The frequency of a pure tone can be discriminated, presumably on the basis of pitch, as soon as it is detectable (Pollack 1947; Cardozo 1974; Gockel et al. 2006). Indeed, pitch may be the cue that allows us to detect a tone in noise (Moore 1981; Carney et al 2002). Frequency discrimination is less good at low levels (e.g. Wier et al. 1977) or high levels (e.g. Bernstein et al. 2006), but the value of the pitch changes with level by at most a few percent for pure tones, and even less for

complex tones (Hartmann 1997). This is remarkable in the face of the strong level-dependency of several physiological responses to sound that have been considered as candidate substrates for pitch perception (Winter 2005).

Frequency discrimination is possible for stimuli as short as one or two cycles (Mark and Rattay 1990), although at such short durations it is uncertain whether discrimination is based on pitch or timbre changes (Hartmann et al 1985). A clear tonal percept requires a longer stimulus (Mark and Rattay 1990; Robinson and Patterson 1995). For very short stimuli, the value of the pitch may differ according to the duration, or the shape of the temporal envelope, but the differences are no more than a few percent (Hartmann 1978; Hartmann et al 1985). As stimuli are made longer, frequency discrimination becomes more accurate (Moore 1973; White and Plack 2003; Gockel et al 2007; Hsieh and Saberi 2007) (Fig. 2).

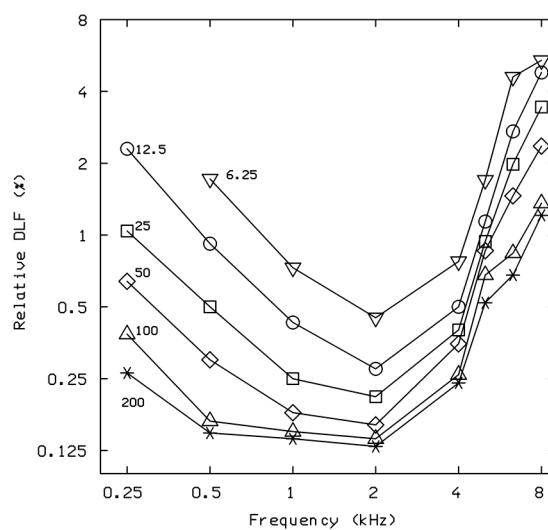


Fig. 2. Frequency difference limens (smallest detectable relative frequency difference) for pure tones. Each curve is for a different stimulus duration (in ms). Discrimination is best for frequencies near 2 kHz and degrades rapidly above 4 kHz. Discrimination is better for longer durations. From Moore (1973).

For stimuli with only low-order harmonics, differences in their relative phase are imperceptible, as stated by Ohm's acoustic law. With higher harmonics (closer-spaced relative to their frequencies), phase may affect the *timbre* of the stimulus, but usually not the value of its pitch. Phase may however affect the *salience* of the pitch, and it may also change the relative weight of competing pitch candidates in stimuli with ambiguous pitch. For example, the pitch of a stimulus with closely spaced partials may be one octave higher if phases alternate between sine and cosine (as illustrated in Fig. 1e), than if they are all sine or all cosine (as illustrated in Fig. 1f). In a few rare situations one may observe small phase-dependent shifts of the value of the pitch (Plomp 1967b; Pressnitzer et al. 2002).

Pitch is evoked by many periodic stimuli, with very different spectra, but not all: some periodic stimuli evoke a pitch that is weak or absent. The

stimulus parameter space has many dimensions, and therefore it is not straightforward to map the limits of the existence region. Roughly speaking, a complex tone may fail to evoke a pitch if (a) its period is too long (Pressnitzer et al. 2001), or (b) the *rank* of its lowest harmonic is too high, or (c), the *frequency* of its lowest harmonic is too high. These limits depend somewhat on the total number of harmonics within the stimulus: they are narrower for two adjacent harmonics (Smoorenburg 1970) than for three harmonics (Ritsma 1962; 1963) or more. There are also interactions between parameters, for example musical pitch extends to a lower F_0 (30 Hz) for a wideband stimulus than for a 3200 Hz high-pass stimulus (270 Hz) (Fig. 3) (Pressnitzer et al. 2001).

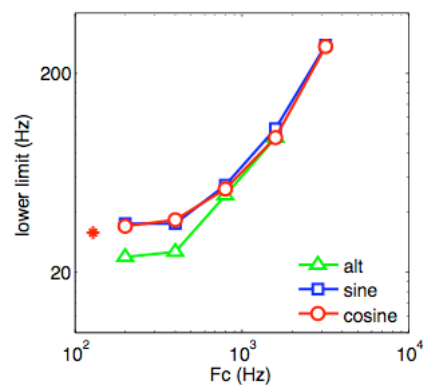


Fig. 3. The lower limit of melodic pitch as a function of the frequency of the lowest partial (F_c) and for different phase relationships: sine, cosine, and alternating sine and cosine (alt). The asterisk is for wideband cosine phase stimuli (click trains). Mean of three subjects. Replotted from Pressnitzer et al. (2001).

Tones with the same period but different spectral envelopes usually evoke the same pitch, despite large timbre differences. It is nevertheless more difficult to match the pitches of stimuli that occupy distinct rather than overlapping spectral regions (Micheyl and Oxenham 2004). Such is notably the case when a pure tone is matched to a complex tone (Moore et al 1992). This difficulty might be due to perceptual interference from the salient difference in timbre, or it might result from the lack of overlap within an internal tonotopically organized representation of stimuli, or both.

For wideband stimuli, with partials spread over a wide frequency range, the various spectral regions carry unequal weight. One way to reveal this is to mistune the frequency of one partial of the complex and observe the shift in the overall pitch. This effect is appreciable only if the partial falls within the *dominant region*. The extent of this region depends on the F_0 : below 50 Hz partials beyond the 6th are dominant (Moore et al. 2007), above 1400 Hz the fundamental is dominant, and in the intermediate range the dominant partials are usually between 2 and 6 but with considerable interindividual differences (Plomp 1967a; Moore et al 1985b).

Pitch may be evoked by stimuli that are only imperfectly periodic such as "iterated rippled noise", IRN. IRN is obtained by delaying a segment of white noise repeatedly, and adding together the delayed and non-delayed waveforms (Yost 1996; Hartmann 1997 chapter 15). Pitch may also arise with stimuli that are, strictly speaking, aperiodic such as amplitude-modulated white noise (Burns and Viemeister 1976). It is as if the auditory system searches for the best periodic approximation to the stimulus, according to some metric that tolerates various forms of mismatch. The same stimulus might allow multiple matches, in which case its pitch may be ambiguous. For example a complex tone with a narrow spectral peak or "formant" (Fig. 1c) may evoke a pitch that fits that peak. This high pitch, corresponding to the formant, may compete with the low pitch corresponding to the F_0 , particularly if the F_0 is relatively low and constant, and the frequency of the spectral peak varies. This effect is exploited in overtone singing (Bloothoof et al 1992).

To summarize, pitch may be evoked by a very wide range of stimuli. Pitch depends mainly on the period ($1/F_0$) and is remarkably insensitive to changes along other stimulus dimensions that provoke salient changes in qualities other than pitch. A very wide range of different stimuli map to the same pitch. This is possibly the hardest to explain: how does the auditory system perform tasks that require accurate discrimination using pitch, while ignoring the very salient effects of differences along other stimulus dimensions? Pitch theories need to explain both the accuracy and the constancy of pitch perception.

4 The pure tone

Much of the psychoacoustics of pitch has been established using pure tone stimuli with sinusoidal waveforms (Fig. 1a). A pure tone evokes a pitch similar to other periodic stimuli of the same period (e.g. Fig. 1b-f). However two things make pure tones "special", and set them apart from stimuli with complex spectra. The first is their special status for the physics and mathematics of sounds. The second is that a pure tone produces essentially the same shape of vibration at every point of the cochlea, albeit with different amplitude and phase.

Sinusoids (more precisely: complex exponentials) are eigenvectors of linear transforms. This means that a pure tone remains a pure tone after propagation through air, reflection from obstacles, or mechanical transmission within the ear. The amplitude and phase of the waveform may be affected by the filtering involved, but it retains a sinusoidal shape, and its frequency remains the same. Furthermore, according to Fourier's theorem any waveform may be decomposed into a sum of such sinusoids. Sinusoids are not the only functions to allow such a decomposition, but their mathematical properties make them a good basis of "elementary waveforms" from which other waveforms can be built.

It is tempting to assume that, just like a complex stimulus is a sum of sinusoids, the percept that it evokes too is the sum of *elementary percepts* evoked by its sinusoidal components. If this were the case psychophysics would be very much simplified indeed: we would need only to study effects

of pure tones to predict the effect of a stimulus of arbitrary complexity. To some extent, psychoacoustics has progressed on the basis of this assumption, witness the large proportion of studies involving pure tones. The idea was inspired by the intense development of harmonic analysis between the 17th and 19th centuries that culminated in Fourier's theorem, that Ohm (1843) and Helmholtz (1877) extended to the sensory domain (Darrigol 2007; de Cheveigné 2005). The same idea is embodied in the "virtual pitch" theory of Terhardt (1974, 1979), according to which the pitch of a complex tone is composed from "spectral pitches" evoked by its partials.

Unfortunately, there is little to support this idea. Introspection tells us that the percept evoked by a complex tone differs radically from the percepts evoked by its sinusoidal parts in isolation. It requires some faith to believe that one is *composed* of the others. True, we can sometimes focus our attention and "hear out" an individual partial, but this requires skill and training, and it succeeds only in particular situations. The issue of hearing out multiple pitches is addressed in Section 6.

Anticipating that discussion, note that a complex tone causes different parts of the cochlea to vibrate with different waveforms depending on which stimulus components are reinforced by cochlear filtering (See Fig.4 in Section 7 below). In particular, some channels may respond mostly to a single resolved partial (e.g. 3rd harmonic in Fig.4). If we suppose that attention can be focused on that subset of cochlear channels, it may be possible to hear out the partial as originally reported by Mersenne (1638), or instead possibly a "residue" of unresolved partials described by Schouten (1940). In the case of a pure tone, however, all parts of the cochlea respond with the same waveform, so attending to a subset of channels should not produce a different percept. In this sense a pure tone is "pure". Pure tones are elementary in that they cannot be partitioned in this way, not in that the percepts that they evoke compose those evoked by more complex sounds. Studies that use pure tone stimuli are informative for those particular stimuli, and by extension for the wider class of periodic stimuli that they belong to, but they do not really probe the "elements" of perception of sound.

The value of the pitch of an arbitrary stimulus has been defined as the frequency of the pure tone to which it can be matched (Hartmann 1997). This provides a convenient means to quantify pitch. However, the pitch of a pure tone varies with sound level and across ears (Burns 1982), at low frequencies a pure tone must have a high amplitude to compensate for the high-pass characteristics of the middle ear (this may introduce distortion products), and for F0s below 2 kHz frequency discrimination is less accurate for pure than for complex tones (Henning and Grosberg 1968). The presence of noise induces pitch shifts that tend to be larger for pure tones than complex tones (Houtsma 1981). For all these reasons, it would make sense to replace the pure tone standard by a complex tone standard, for example a click train.

Studies that use only pure tones do not probe the property of invariance across stimuli with different spectral content. This is a concern for physiological and brain imaging studies, as it may be uncertain that a response reflects pitch rather than some other correlate of stimulus manipulation.

To summarize, pure tone stimuli are illustrative of a wider class of pitch-evoking stimuli, but there is little reason to think that the percept evoked by a complex sound is *composed* of the percepts evoked by each of its sinusoidal components. Studies that aim to establish that a response reflects pitch need to use a wider range of stimuli.

5 The missing fundamental

Rarely has a paradox provoked such a long-lasting and heated debate. The pitch evoked by a pure tone remains the same if we add additional tones with frequencies that are integer multiples of that of the original pure tone (harmonics). It also does not change if we then remove the original pure tone (the fundamental): this is the "paradox" of the missing fundamental. At issue is whether, and how, a periodic tone that lacks a sinusoidal component at its F_0 can evoke a pitch. Concerning the stimulus itself there is no paradox: Fourier's theorem states that a periodic waveform is composed of sinusoids with frequencies that are integer multiples of F_0 , but it does not say that they must *all* be present. Compare for example the waveforms of Fig. 1(b) and Fig. 1(c): both are clearly periodic. Concerning the percept, the paradox vanishes if one accepts that pitch is associated with the *periodicity* of the stimulus. The paradox appears only if we insist that pitch requires the presence of a sinusoidal fundamental component.

The psychophysics is quite clear: the presence of a fundamental component is not required for pitch. This was established already in the 19th century by Seebeck, who synthesized stimuli where the fundamental was weak or absent (de Boer 1976; Turner 1977). It was confirmed by Schouten (1938) who addressed the issue of a possible distortion product (created within the apparatus or within the ear) by adding to the stimulus a sinusoidal component with carefully controlled amplitude and phase to cancel any remaining energy at the F_0 . Licklider (1954) corroborated his conclusion by adding low-pass noise to mask any distortion products, and this has since been replicated in hundreds of studies. There is little support for Ohm's dogma according to which pitch requires a sinusoidal component at the fundamental.

In spite of all this evidence, there is a reluctance to abandon this idea. The observation of fundamental components in the analysis of physiological recordings (where they arise naturally as the result of nonlinearities), or the demonstration that relatively high-amplitude distortion products may arise in the ear (Pressnitzer and Patterson 2001), keep alive the suspicion that the fundamental might sneak into the ear unnoticed. However the most potent reason to retain Helmholtz's picture of the ear as a Fourier analyzer is that it is too attractive to abandon. The missing fundamental will be with us for some time.

6 Hearing out pitch

We are adept at *hearing out* sounds, for example a faint voice among the sounds of a forest, or the melodic line of an instrument within the orchestra.

We usually study pitch in relation to the acoustic waveform, but in real life it often emerges from a fraction of the stimulus, the rest constituting a masker to be ignored. The masker itself may include one or more pitch-evoking sources, as in music when several instruments play at the same time. In order to hear each pitch, the ear must overcome masking from the energy of the competing sounds ("energetic masking"), and also ignore the percepts that those sounds evoke ("informational masking"). This is an example of the process of Auditory Scene Analysis (Bregman 1990) by which we parse an acoustic scene and attend to its parts. There are large interindividual differences in the susceptibility to informational masking, musicians being more adept at focusing on a frequency range than non-musicians (Oxenham et al 2003).

Despite its obvious musical relevance, the psychoacoustics of competing pitches is surprisingly sparse (Beerends and Houtsma 1989; Carlyon 1996a; Assmann and Paschall 1998; Micheyl et al. 2006b). If several partials of a tone dominate part of the spectrum, such that they are resolved by at least some cochlear channels, the ear may be able to focus on that tone and ignore the others. For example in polyphonic music, the spectrotemporal envelope of one voice may have "windows" of low energy within which the other voices may be glimpsed in this way. However, experiments have shown that concurrent tone pairs that overlap in both frequency and time may also evoke salient pitches, as long as their partials are sufficiently spaced to be *resolvable* by cochlear filtering (Carlyon 1996a; Micheyl et al. 2006b). In contrast, if two tones contain only unresolved partials, mixing them gives rise to a noiselike sound or "crackle" (Carlyon 1996a), unless one is stronger than the other in which case only one pitch is heard (Micheyl et al. 2006b). The concept of resolvability is discussed in more detail in Section 7. In summary, it is often possible to hear out a pitch from a background of interfering sounds, some of which may themselves evoke a pitch.

Pitch is nevertheless degraded by sounds presented simultaneously, or even sequentially in close temporal proximity. Presenting temporal "fringes" before or after a stimulus degrades discrimination (Carlyon 1996; Micheyl and Carlyon 1998), apparently because information from the fringes leaks into the integration window that sums pitch information over time. Likewise, a distractor tone presented simultaneously in a remote frequency region produces what is known as "pitch discrimination interference" (Gockel et al 2004; Micheyl and Oxenham 2007). The degree of interference depends on both *spectral proximity* and *pitch similarity*, suggesting that interference may occur at two stages: within a tonotopically-organized low-level representation of the signal, and within a higher-level representation of pitch (or yet higher levels such as attention, etc.).

If the masker is a noise band that overlaps the target in time and frequency region, the pitch of the target may be discriminable as soon as the target is detectable (Moore and Glasberg 1991; Micheyl et al 2006b; Gockel et al 2006). It is as if the cue for detecting the tone within noise were pitch. In contrast, if the masker is a complex tone, the detection threshold is about 15 to 25 dB *below* the level at which the target's pitch can be discriminated (Micheyl et al 2006b). The detection cue here is more likely the disruption of the tonal percept evoked by the masker. These phenomena are of interest because they may shed light on how pitch is extracted and represented within the auditory system.

Perhaps the earliest report of multiple pitches within the same sound is that of Mersenne (1636), who heard, within the sound of a plucked string, "at least five sounds" corresponding to the fundamental and first few harmonics. Hearing out partials requires concentration and training: Sauveur (1701) recommended listening at night, while Helmholtz (1877) relied on special resonators that he designed to enhance the partials. The task is easier for harmonics of low rather than high rank. Estimates of the highest audible partial vary according to the method employed, ranging from the 5th to 8th (Plomp 1964) or the 9th to 11th (Bernstein and Oxenham 2003). They are roughly consistent with the hypothesis that a partial may be heard out if the distance from its closest neighbor is greater than about 1.25 ERB (Moore and Ohgushi 1993; Moore et al. 2006) (the equivalent rectangular bandwidth, ERB, is a measure of cochlear filter width, Moore and Glasberg 1983). Hearing out partials is easier for tones of long rather than short duration (Gockel et al 2007). It is also easier if the partial is mistuned from the harmonic series, or amplitude-modulated, or turned on later than the rest of the complex tone (Peters et al. 1983; Moore et al 1985a; Hartmann and Doty 1996; Bernstein and Oxenham 2003; Hartmann and Goupell 2006).

Although partials of a complex may be heard out with effort and attention, they are rarely salient spontaneously unless enhanced by some spectral or temporal irregularity (Hartmann and Goupell 2006; Bernstein and Oxenham 2003). Listeners differ in their propensity to listen to a complex tone as a whole ("synthetic listening") or as composed of parts ("analytic listening") (Smoorenburg 1970; Laguitton et al 1998). Audibility of partials inspired the doctrine according to which the percept of a complex tone is composed of the percepts of its partials, but an alternative interpretation is that the ear, being adept at hearing out weak sounds within a background, can sometimes perform this feat with the partials that compose a complex tone.

7 Resolvability

An important concept, already mentioned, is *resolvability*, the ability of cochlear filtering to isolate individual partials of a complex sound. A partial is resolved if it is sufficiently remote in frequency from other partials so that it dominates the response of at least some cochlear filters. By extension, a complex stimulus is said to be "resolved" if it contains at least some resolved partials (and "unresolved" if it contains none). Figure 4 illustrates the concept for a 30-component complex tone with 100 Hz fundamental. Each of the lowest 3 to 5 partials dominates the output of a few filters, near the apex of the cochlea. The output of these filters is quasi-sinusoidal at the frequency of the partial (Fig. 4 bottom left): these partials are resolved. Partial of higher rank are less well isolated: the best filter contains a large proportion of power from other components, and the output waveform is more strongly modulated and less sinusoidal (Fig. 4 bottom right). Partial such as these are unresolved. As an aside, we note that the uppermost partial of this complex is comparatively well isolated, which might account for the relatively salient pitch of the highest partial of such a complex (Moore et al 2006).

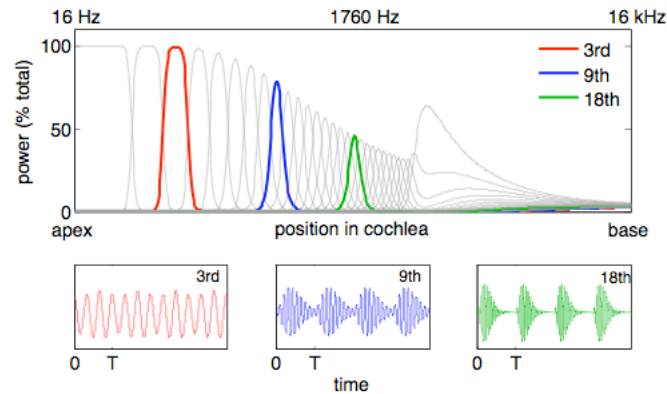


Fig. 4. Resolvability of harmonics of a complex tone. Top: percentage of power for each harmonic of a 30-component complex tone at the output of cochlear filters, plotted as a function of their position along the cochlea. The apex of the cochlea is tuned to low frequencies (left) and the base to high frequencies (right). Bottom: waveforms at the output of filters tuned to the 3rd harmonic, 9th harmonic and 18th harmonic. Each of the lower harmonics is isolated within a set of filters near the apex of the cochlea (left of upper plot). The output of these filters is quasi sinusoidal (bottom left): the lower harmonics are "resolved". Each of the higher harmonics excites a narrower range of filters (middle and right of upper plot). Outputs of these filters are "pulsatile", indicating that the filters respond to more than one harmonic: higher harmonics are "unresolved". The cochlea is modeled here as a bank of linear 4th-order gammatone filters uniformly spaced in terms of equivalent rectangular bandwidth (ERB, Moore and Glasberg 1983), which is roughly equivalent to uniform spacing along the cochlea.

Resolvability determines, in part, whether partials of a complex tone can be "heard out". It also seems to play a role in the pitch of the complex as a whole: stimuli with one or more resolved partials tend to have a strong pitch, while those with only unresolved partials have a weak pitch. This is puzzling because unresolved partials produce beats along the basilar membrane at the F_0 , and one might expect this to be a clear cue to pitch. Instead, partials of low rank dominate the pitch of a complex (Plomp 1967a; Moore et al 1985b), and F_0 discrimination thresholds are an order of magnitude smaller if the stimulus contain partials below about the 10th (Fig. 5) (Houtsma and Smurzynski 1990; Shackleton and Carlyon 1994; Plack and Carlyon 1995; Bernstein and Oxenham 2003) than if it does not. Accurate discrimination requires longer stimuli for unresolved than resolved partials (White and Plack 2003). The ability to hear the pitches of concurrent complex tones is limited to tones with resolved partials: mixtures of unresolved tones evoke a crackling sound (Carlyon 1996a). All these phenomena hint at a role for resolvability in pitch.

The contrast between performance for resolved and unresolved-partial stimuli has led to the hypothesis that their pitches are processed by

different mechanisms: *pattern matching* for resolved, and *autocorrelation* for unresolved (see Section 9). This necessarily implies also a third mechanism to translate between the two. Indeed, degraded performance in comparing pitch between resolved and unresolved stimuli has been taken as evidence of a translation cost between pitch mechanisms (Carlyon and Shackleton 1994).

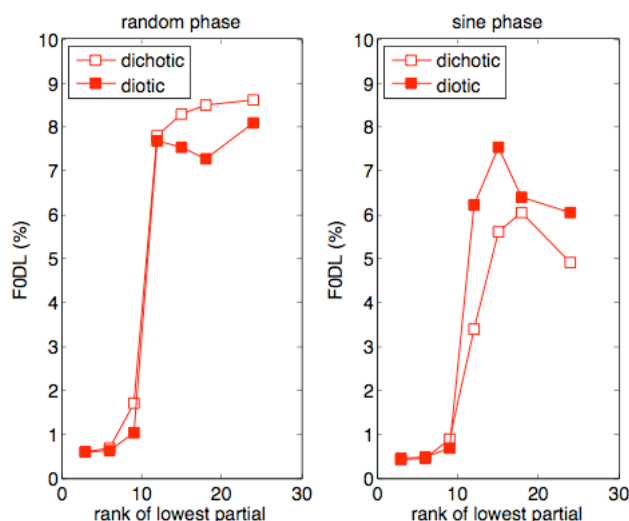


Fig. 5. F0 difference limens for a 200 Hz complex tone as a function of the rank of the lowest partial. Phases were either random (left) or sine (right). In the 'diotic' condition (full markers) all partials were presented to both ears. In the 'dichotic' condition (open markers) partials of odd rank were presented to one ear, and partials of even rank to the other ear. Average of 4 subjects, replotted from Bernstein and Oxenham (2003).

However, several results do not fit with this interpretation: (a) Moore et al. (2007) found for F0s of 35 and 50 Hz that partials with ranks greater than 6 (presumably *unresolved*) dominated the pitch of the complex. This suggests that dominance may depend on a factor other than resolvability. (b) The lower limit of melodic pitch does not coincide with the limit of resolvability: tones that lack any resolved partial may nevertheless evoke a pitch that supports melody (Pressnitzer et al 2001). (c) Bernstein and Oxenham (2003, 2008) found that the deterioration of discrimination thresholds beyond the 10th partial occurred regardless of whether all partials were presented to the same ear (in which case they were too closely spaced to be resolved) or else partials of even and odd rank were distributed to opposite ears (in which case their spacing is doubled, so that partials up the 20th should be resolved according to their criteria) (Fig. 5). Peripheral resolvability is therefore not the factor that determines accurate pitch. (d) It was said earlier that complex tones that are mixed together each evoke a pitch only if they contain resolved partials. However the meaning of "resolved" in that context applied to the complex tones *in isolation*, before

mixing. Obviously after mixing the partials may no longer be resolved. The pitches may nevertheless be salient, so resolvability of partials *within the stimulus* is not crucial (Micheyl et al 2006b). (e) Finally, Micheyl and Oxenham (2004) reexamined the issue of a putative translation cost between distinct pitch mechanisms for resolved and unresolved stimuli, and concluded that there is none (see also Micheyl and Oxenham 2005 and Gockel et al 2004). All these results suggest that peripheral resolvability *per se* is not what determines the salience of the pitch of a complex tone.

To summarize, stimuli with partials of low rank may evoke a pitch that is more salient and accurately discriminable than stimuli that only contain partials of high rank. This is often attributed to differences in resolvability of partials within the complex tones, but this interpretation does not fit some aspects of the data, and other interpretations have been proposed, such as that the duration of internal delays varies according to cochlear filter characteristic frequency (Moore 1982; Bernstein and Oxenham 2005; de Cheveigné and Pressnitzer 2006). The debate is of importance to decide which strategies are used to hear pitch (Section 9).

8 Binaural pitch

Our ears sample the acoustic field in two points, and this helps us to localize sounds and make sense of complex acoustic scenes. Certain pitch phenomena require binaural interaction, and binaural hearing and pitch may actually have something in common. Both seem to be based on temporal cues analyzed within the brain, and two influential models of sound localization (Jeffress 1948) and pitch (Licklider 1951) both postulate neural processing based on time delays and coincidence counting. Experimentally, binaural stimulation adds a degree of freedom that may help us locate the site of pitch extraction within the brain.

Fascinating among auditory phenomena is *Huggins pitch*, which arises while listening with two ears to a binaural stimulus that sounds like noise when listened to with either ear alone (Cramer and Huggins 1958; Culling 1999). Huggins pitch is one of several binaurally created pitch phenomena (see Culling et al 1998 for a review). The stimulus consists of white noise that is identical at the two ears except for a narrow frequency region for which noise is decorrelated between the two ears (for example the noise in one ear may undergo a phase transition of 2π over this frequency region) (Fig. 6). The percept resembles that of a narrowly filtered band of noise, embedded within a wideband noise background. Relatively faint, it nevertheless supports accurate matching (Hartmann 1993). It becomes stronger if multiple transitions occur at frequencies that follow a harmonic series, forming a "Huggins complex tone" (Bilsen 1976). Huggins pitch supports melody (Akeroyd et al 2001), and streaming effects similar to those produced by pure tones (Akeroyd et al 2005). Huggins pitch necessarily arises from the interaction of neural patterns from the two ears, and this puts a constraint on the locus of pitch extraction (see Section 10 below).

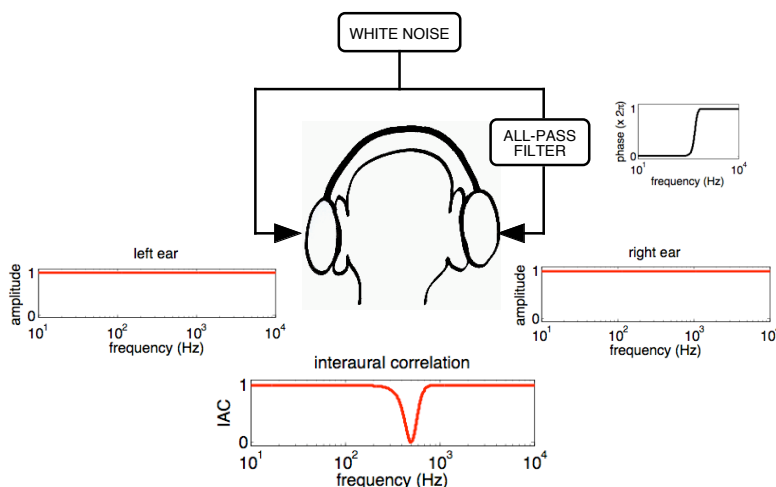


Fig. 6. Huggins pitch is obtained by presenting white noise to both ears. The noises at both ears are identical apart from a narrow phase transition created by an all-pass filter in the pathway to one ear. Interaural correlation is high, except at the frequency of the phase transition. The pitch matches this frequency.

Houtsma and Goldstein (1972) presented musically-trained subjects with pairs of partials that formed "complex tones" with an F0 determined by the largest common divisor of their frequencies. They successfully performed an interval recognition task, showing that they could hear a low pitch related to this F0, regardless of whether the partials were sent both to the same or to different ears. This is a second example of central formation of pitch from information from both ears. Listening to either ear alone, one hears only a single partial and not the low pitch.

Binaural interactions can create pitch, but they can also weaken it. In a study mentioned earlier (Section 7), Bernstein and Oxenham (2003) found that F0 discrimination thresholds of complex tones increased by an order of magnitude when the rank of the lowest harmonic was increased from the 9th to the 12th (Fig. 5). Interestingly, the same occurred when all harmonics went to both ears (diotic condition), or even and odd harmonics to opposite ears (dichotic condition). A complex with even harmonics of F0 starting from the 12th is identical to a complex with all harmonics of 2 F0 starting from the 6th. Listening to that ear alone should therefore give a *low* threshold. The fact that thresholds were instead high implies that the subjects could not shut off the contribution of the other ear. Surprisingly, the additional information from the odd harmonics within the other ear was deleterious rather than useful.

With a slightly different paradigm, in which stimuli were sent to the same ear within blocks, rather than to opposite ears on each trial as in their previous study, Bernstein and Oxenham (2008) did find a benefit of binaural presentation, but still not as great as if the ear receiving the odd harmonics could be ignored. Gockel et al (2005) found that a mistuned partial presented contralaterally to the rest of a complex affected the low pitch, but less than when presented to the same ear. Similarly, Gockel et al (1999)

found that the interference produced by "fringes" that preceded or followed a complex tone was reduced, but not abolished, by contralateral presentation.

Interestingly, the spatial percept also appears to be affected by interactions with pitch. Huggins pitch is hard to localize (Akeroyd and Summerfield 2000). In the well known "octave illusion", Deutsch (1974) found that, when tones of 400 and 800 were presented in alternation such that one ear received the lower when the other received the higher, subjects reported two tones pulsing, the lower tone at one ear and the higher at the other ear. The side that heard the higher tone depended on subject's handedness, and was subject to spontaneous reversals. Interactions between pitch and spatial hearing might arise if they shared physiological substrates (see Section 10).

9 How do we perceive pitch?

How we perceive pitch has been a matter of intense debate for many years (see de Cheveigné 2005 for a review). It is not yet resolved, and so there is no authoritative explanation of how pitch emerges within the auditory system. The best that we can do is to try to understand the positions in this debate. Two properties need explaining: (a) the *sensitivity* of pitch to small changes in **F0**, and (b) the relative *invariance* of pitch to large changes in other stimulus parameters. The second property is less often considered, but it is just as important as the first.

According to the *place* hypothesis (Helmholtz 1877), pitch is determined from the position of maximum excitation along the basilar membrane, within the cochlea. This hypothesis is attractive because it readily accounts for sensitivity: a change in F0 is necessarily accompanied by spectral differences that the excitation pattern should – cochlear frequency resolution permitting – reveal. However the place hypothesis has a harder time accounting for invariance of pitch across stimuli with different spectra, for example the fact that a pure tone and complex tone can evoke the same pitch.

A pure tone evokes a localized peak of excitation along the basilar membrane, and its frequency could conceivably be discriminated on the basis of this cue, or other cues such as changes along the flanks of the peak of excitation as it shifts with frequency. There are some issues with this idea: excitation patterns measured physiologically are rather broad. They tend to broaden and shift with increasing intensity, without commensurable changes in pitch or discrimination acuity (Chatterjee and Zwislocki 1997). The parameter dependence of pure tone pitch discrimination does not fit what is expected of an excitation pattern-based cue (e.g. Moore 1973, Moore and Sek 1995, 1998). These and other considerations argue against the place hypothesis, even in the case of pure tone pitch, except for relatively high frequencies (above about 5 kHz). However, the main problem is that the place hypothesis fails to explain how pure and complex tones might have the same pitch. A complex tone typically evokes multiple peaks, one for each resolved partial (or group of unresolved partials), so the hypothesis needs amending to address this situation. The solution proposed

by Ohm (1844) and Helmholtz (1877) was to assume that the pitch of the complex is determined by the peak associated with its *fundamental* partial. That solution floundered on the missing-fundamental phenomenon mentioned previously.

According to the *time* hypothesis, pitch is derived from the periodic pattern of the acoustic waveform, transduced by the cochlea into a pattern of nerve pulses that is processed by the brain. The appeal of this hypothesis is that pitch maps more directly to the stimulus period than to spectral features such as the – possibly missing – fundamental. However, the hypothesis is also incomplete: we still need to explain how the ear reliably extracts one pulse per period, how the pulses are transmitted to the brain, and how the brain counts them. The second point once was contentious because nerve fibers cannot transmit spikes at rates beyond a few hundred spikes per second. This issue was resolved by Wever and Bray (1930) who pointed out that higher rates can be transmitted collectively by groups of fibers. Today it is accepted that periodicities may be coded by the instantaneous probability of spikes within groups of auditory nerve fibers (up to about 5 kHz in cat, Johnson 1980).

The main difficulty with the time hypothesis is that it is not easy to extract one pulse per period, in a way that is reliable and fully general. If we were dealing only with pure tones, then we could postulate some mechanism that triggers a pulse on a peak, or a zero-crossing of the waveform. However complex tones often have several peaks and/or zero crossings per period. Furthermore the position and number of such cues is highly phase-dependent, which is hard to reconcile with the largely phase-independent nature of pitch (Wightman 1973a). In their simplest form, place and time hypotheses both have insurmountable difficulties in accounting for pitch. Both explain sensitivity to variations in period, but not invariance across stimuli with same period. The debate has now shifted to two newer models, *pattern matching* and *autocorrelation*.

According to the pattern matching hypothesis, pitch is associated with the harmonic pattern of the partials. The ear is assumed to contain a dictionary of *harmonic templates*, against which the incoming patterns of frequencies are compared. The template that best matches the pattern indicates the pitch. Pattern matching was proposed by de Boer in his thesis (1956) and later promoted by Wightman (1973b), Goldstein (1973) and Terhardt (1974), but the seeds of the idea were already in Helmholtz's concept of *unconscious inference* according to which perception proceeds by matching internal models against incoming sensory evidence. Helmholtz in turn borrowed it from Alhazen who had formulated it in the 11th century (Hatfield 2002).

Pattern matching allows the place hypothesis to be salvaged by assuming that individual partials (not just the fundamental) give rise to local peaks in excitation along the basilar membrane. For that reason it is sometimes equated with the "place" hypothesis. However pattern matching is also compatible with the time hypothesis, if one supposes that frequencies of individual partials are extracted from the temporal patterns that they produce locally at different points along the basilar membrane (supposing that they are resolved). The pattern matching mechanism ensures invariance across stimuli of differing spectra (but same F0), and in particular it solves the "paradox" of the missing fundamental. For example a set of partials at

200, 300 and 400 Hz would trigger the same harmonic template as a 100 Hz pure tone, or any other complex of same period.

The pattern matching hypothesis works if enough partials are resolved so as to constrain the choice of template (Section 7). However, pitch is known to arise also for stimuli for which there are no resolved partials. Pattern matching cannot account for such a pitch. This would bring us to discard the hypothesis, if it were not for three conjectures that might save it. The first is that human cochlear frequency resolution might somehow be finer than usually assumed (e.g. Oxenham and Shera 2003). The second is that stimuli with non-resolved partials might produce distortion products that are resolvable. The third is that pattern matching might coexist with some other mechanism (see below).

The *autocorrelation* hypothesis differs from the time hypothesis in that it does not require spikes to be triggered at a well-defined position within the period. Rather, the periodic neural pattern is processed by coincidence-detector neurons that calculate the equivalent of an autocorrelation function (Licklider 1951, 1959; Meddis and Hewitt 1991a, b; Cariani and Delgutte 1996a, b). The spike trains are delayed within the brain by various time lags (using neural delay lines) and combined or correlated with the original. When the lag is equal to the time delay between spikes the correlation is high and outputs of the coincidence detectors tuned to that lag are strong. Spike trains in each frequency channel are processed independently and the results combined into an aggregate pattern (Fig. 7). In response to a periodic tone, a ridge appears in the pattern at a lag equal to the period, and this is the cue to pitch. This cue appears for stimuli with *unresolved* partials because the partials beat together at the fundamental (Fig. 7 right column). It also appears for stimuli with only *resolved* partials (which produce no beating at the fundamental period in any peripheral channel). This happens because all partials are multiples of the same F_0 , and therefore share a common period multiple equal to $1/F_0$ (Fig. 7 middle column).

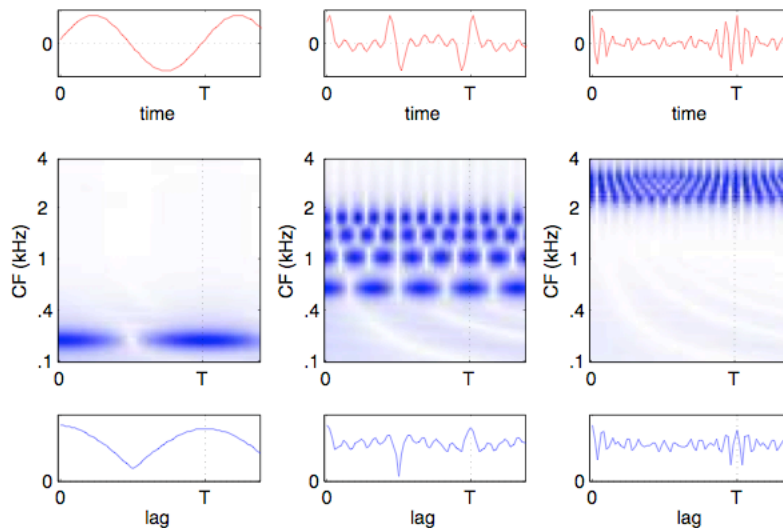


Fig. 7. Autocorrelation model of pitch. Top: acoustic waveforms, middle: array of autocorrelation functions (ACFs), bottom: summary autocorrelation functions (SACFs). Stimuli were: 200 Hz pure tone (left column), 200 Hz complex tone with partials 3, 5, 7, 9 (central column), and 200 Hz complex tone with partials 12, 13, 14, 15, 16 (right column). For the central column, we chose a complex tone with well-spaced partials to illustrate the point that salient within-channel F_0 cues are not necessary to produce a salient F_0 cue in the overall pattern (middle row) or summary (bottom row). The autocorrelation model was modeled with a linear gammatone filterbank followed by half wave rectification, calculation of a running autocorrelation function, cubic root compression, and summation over filter channels. The cue to pitch is the position of a ridge across channels in the ACF pattern (middle) or a peak in the SACF (bottom).

The autocorrelation process is insensitive to phase, and this addresses the objection against time models mentioned earlier. Phase sensitivity may nevertheless arise from nonlinearities in its physiological implementation, see Section 10. Coincidence detection is plausible in terms of known physiology, but the hypothesis also requires *neural delays* of up to about 30 ms (to cover the range of musical pitch down to 30 Hz). There is little direct evidence for neural delays that long (Winter 2005, but see de Cheveigné and Pressnitzer 2006). Autocorrelation is theoretically related to pattern matching (de Cheveigné 1995), and indeed it could be proposed that autocorrelation is the way pattern matching is implemented in the brain: the two hypotheses are not necessarily mutually exclusive.

An argument sometimes made against autocorrelation is that it works too well: it predicts that pitch should be equally salient for stimuli with resolved and unresolved partials, whereas we saw that such is not the case. This led to the *multiple-mechanism hypothesis*, already mentioned in Section 7, according to which pattern-matching explains the strong pitch of stimuli with resolved harmonics, and autocorrelation the weaker pitch of stimuli with only unresolved harmonics (or electrical stimulation in cochlear implantees). The alternative to two mechanisms is that a *unitary model* can account for all aspects of pitch (Meddis and Hewitt 1991; Meddis and O'Mard 1997). This debate is fueled by recent work on the psychophysics of resolved vs unresolved stimuli (Section 7).

In addition to these main theories (place, time, pattern matching, autocorrelation) there are many variants such as the strobed temporal integration model of Patterson et al. (1992) or the cancellation model of de Cheveigné (1998). They address the two main aspects of pitch mentioned at the beginning of this section: (a) sensitivity of pitch to F_0 , (b) invariance across stimuli with the same F_0 . Other aspects that also need explaining are (c) how we perceive pitch in the presence of other sounds, (d) musical properties such as harmony, and (e) the detailed aspects of pitch reported in the psychophysics literature. We are unfortunately rather far from a complete answer to the question "how do we perceive pitch?".

10 The physiological basis of pitch perception

Sound entering the ear is transduced within the cochlea into neural patterns that are processed at several stages within the brainstem, thalamus and cortex. Each of these stages could be involved in pitch perception, either as processing stage or as a relay of relevant information.

The cochlea is sometimes likened to a "spectrum analyzer" that transforms the sound waveform into a spectrum coded as a profile of discharge rate across the auditory nerve. However the auditory system also has access to the temporal patterns (so-called *fine structure*) at the output of each filter, and one could propose instead that the role of the cochlea is to transduce acoustic vibrations into temporal patterns of neural firing. According to this hypothesis, the role of cochlear selectivity would be to improve the quality of transduction and assist scene analysis (de Cheveigné 2001). These two views (spectrum analyzer vs frequency-selective transducer) map to the "place" and "time" hypotheses. How do they fit with what we now know about cochlear filter properties?

Our knowledge is inferred mainly from psychophysical studies in humans (Patterson 1976; Glasberg and Moore 2000) and measurements from the basilar membrane or the auditory nerve in animals (Robles and Ruggero 2001; Ruggero 1992; Cedolin and Delgutte 2005). The results are roughly consistent across species (Ruggero and Temchin 2005), but there are wide differences in estimates of cochlear filter bandwidth depending on the technique used. For example, bandwidths measured psychophysically (in humans) in forward masking experiments are narrower than those measured with simultaneous masking by a factor of up to two (Oxenham and Shera 2003). Likewise, auditory nerve fiber tuning curves measured with pure tones are considerably narrower than transfer functions estimated by the reverse correlation technique using noise stimuli (Carney and Yin 1988). This is a problem for our purpose, because the plausibility of different hypotheses depends crucially on the available selectivity.

We can attempt to make sense of these conflicting estimates by recalling that cochlear filtering involves a non-linear active process. In response to a weak *isolated pure tone* at the best frequency of the measurement site, the gain of the cochlear amplifier is large. The gain decreases as the level of the tone increases, implying a concomitant reduction in selectivity (Robles and Ruggero 2001). The gain also decreases if a second, off-frequency pure tone is added to the on-frequency probe, a phenomenon known as two-tone suppression (Ruggero et al. 1992; Jülicher et al 2001). Thus, pure-tone tuning curves may reflect a sharp selectivity that is available only for isolated pure tones at threshold, and not for more complex stimuli. This would explain the much-wider estimates obtained with reverse correlation using wide-band noise stimuli, and also possibly the discrepancy between psychophysical estimates of selectivity from simultaneous and forward masking (Oxenham and Shera 2003). When speaking of cochlear selectivity as applies to pitch, we must be careful to distinguish between the case of isolated pure tones and that of individual partials of complex tones. Selectivity is less good for the latter.

How does this relate to our different pitch theories? The *place* hypothesis assumes a peak of excitation along the basilar membrane. This is

plausible for pure tones at low levels, but at higher levels the peak becomes broader and tends to shift towards a lower frequency place. By contrast, the pitch is rather stable with increasing intensity. For complex tones, it is unlikely that accurate estimates of the frequencies of individual partials, required by the pattern matching hypothesis, can be derived from peaks in a rate-place representation (but see Cedolin and Delgutte 2005). They could, however, be derived from *temporal cues*, supposing that each partial is resolved at some point along the basilar membrane so that its periodicity can be measured without interference from its neighbors (Section 7, see also Fig. 7 middle column). It has also been suggested that the *phase* characteristics of the cochlear filter may contribute to the estimation of the frequencies of individual partials (Shamma and Klein 2000). Cochlear selectivity is not essential for the *time* and *autocorrelation* hypotheses, but it may facilitate hearing out the pitch of a sound in the presence of competing sounds by improving the signal-to-noise ratio within individual channels (de Cheveigné 2001). To summarize, cochlear frequency analysis certainly plays an important role in pitch perception, but there is little support for the idea that pitch is derived from peaks in a place-rate representation.

At each point along the basilar membrane, the acoustic stimulus gives rise to vibrations that are transduced into a pattern of firing ("spikes") within the auditory nerve. The occurrence of each spike is random, but the *instantaneous probability* of occurrence is not: it follows roughly the half-wave rectified waveform of the mechanical vibration at each locus of transduction. The shape of that vibration reflects the stimulus (spectrum, amplitude), but also the filtering and non-linear properties of the cochlea. For a periodic stimulus, the overall discharge pattern is periodic in terms of instantaneous probability.

For a *pure tone*, basilar membrane vibration is sinusoidal, narrowly localized for a low amplitude tone, and more spread out for a louder tone. The phase of vibration varies along the basilar membrane, slowly from stapes to just before the locus of maximal sensitivity, and more rapidly thereafter. Thus, there is a phase shift across the population of fibers that respond to a pure tone. The pitch of a pure tone could be derived by measuring the period of the discharge probability, or by locating the point of most rapid phase transition (this is a "time"-based version of the place hypothesis) (Shamma and Klein 2000).

For a *complex tone*, there are three cases of interest. A locus that responds to a partial of low rank may vibrate sinusoidally at that partial's frequency (Fig. 4 bottom left). A locus that responds to a *combination tone* produced by cochlear distortion may likewise vibrate sinusoidally at the frequency of that combination tone. Other loci, that respond to multiple partials, may vibrate with a complex waveform with an envelope period equal to the fundamental (Fig. 4 bottom, middle and right panels). Thus there are multiple temporal cues within the discharge pattern of auditory nerve fibers that could support the pitch of a complex tone.

Phase-locking of spike trains to the stimulus decreases as stimulus frequency is raised, and is no longer measurable beyond about 5 kHz in cat (Johnson 1980). The limit is lower in guinea pig (Palmer and Russell 1986), higher in the barn owl (9 kHz, Köppl 1997) and unknown in humans (Fig. 8). A small synchronization index does not necessarily imply that all temporal information is lost: a modeling study based on Johnson's cat data

found that residual temporal information might be useful up to 10 kHz (Heinz et al 2001). As one proceeds to higher relays within the auditory system, synchrony is limited to yet lower frequencies.

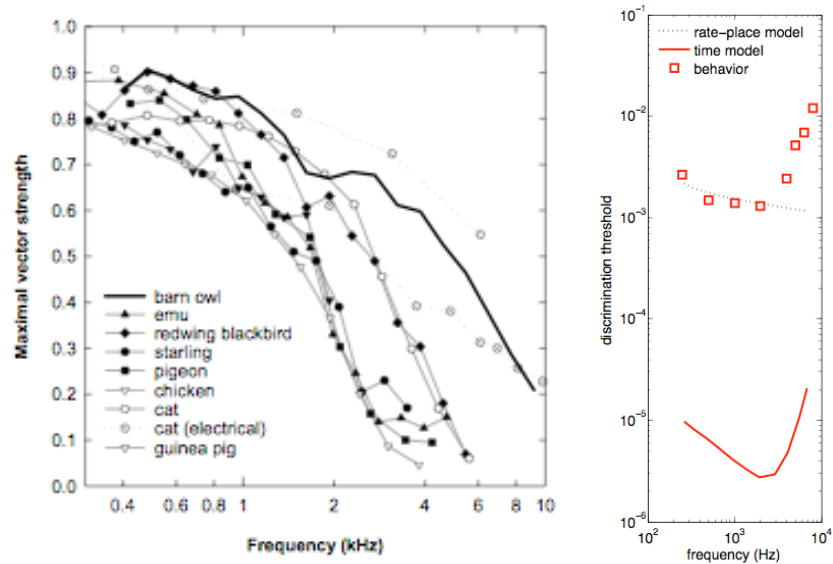


Fig. 8. The synchronization index (or vector strength) is used as a measure of quality of the temporal information carried by auditory nerve fiber discharge patterns. It is plotted here as a function of stimulus frequency for several species (reproduced from Köppl 1997). A higher value indicates a better representation of a pure tone of that frequency. Data labeled 'electric' are for electric stimulation of the auditory nerve (see Köppl 1997 for references). Right: human pure tone frequency discrimination thresholds (symbols) and predictions by a place-rate model (dashed line) and a temporal model fit to cat synchronization data (full line), replotted from Heinz et al (2001). Loss of synchrony at high frequencies produces a degradation of predicted thresholds that parallels that observed behaviorally in humans. However the predicted thresholds are two orders of magnitude too good: to account for this discrepancy would require the additional assumption of a uniformly inefficient processing of temporal information. The place-rate model does not predict higher thresholds at high frequencies.

Where are temporal cues processed? Obviously this can only occur at a level within the nervous system where they are accurately represented. Auditory nerve fibers terminate within the cochlear nucleus, and from there they are relayed to a series of nuclei within the brainstem and midbrain, that themselves project to the auditory thalamus and cortex. Specializations for time are observed at several levels. For example within the cochlear nucleus (CN), bushy cells are fed from auditory nerve fibers via large synapses, so that their activity resembles that of their afferents with little loss of temporal accuracy (so-called "primary-like" response). Other cells (stellate-D and octopus) discharge accurately on the onset of a stimulus, or at each period of wideband stimuli such as click trains. These cells project to multiple nuclei within the superior olivary complex and lateral lemniscus (LL) (Fig. 9).

Spherical bushy cells within CN project bilaterally to the medial superior olive (MSO) and ipsilaterally to the lateral superior olive (LSO), as well as to other nuclei of the superior olivary complex (SOC) and LL. Globular bushy cells within CN project to the contralateral medial nucleus of the trapezoid body (MNTB) via secure synapses that ensure are relayed reliably and with low jitter. In turn MNTB neurons, which are inhibitory, project to ipsilateral LSO and other nuclei within SOC and to the ventral nucleus of the lateral lemniscus (VNLL), that also receives input from octopus cells of the cochlear nucleus via large synapses. Octopus cell projections to VNLL are numerous in man (Adams 1997). All of these nuclei, and others within the brainstem, receive input from temporally-specialized cochlear nucleus cells (Thompson and Schofield 2000). Some of these nuclei, such as MSO, MNTB and LSO, are thought to subserve binaural processing, but this does not preclude them from other tasks that involve temporally accurate patterns, such as pitch processing. Ascending projections from these nuclei mostly terminate in the inferior colliculus (IC) (Ehret 1997).

Cells within IC and beyond synchronize to stimulus periodicities of at most a few hundred Hertz (Liu et al 2005). Therefore it is likely that fast temporal processing is performed at a lower level: *subcollicular* nuclei are potential substrates for the signal processing operations required by pitch.

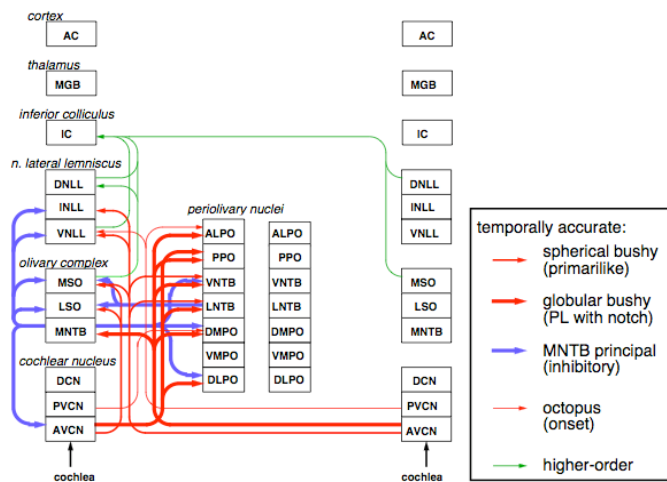


Fig. 9. Temporally specialized pathways within the auditory brainstem and midbrain. Spike patterns from the cochlea are relayed by several types of cell within the cochlear nucleus (CN): globular bushy (thick red) and spherical bushy (medium red), with firing patterns similar to auditory nerve fibers. Globular bushy cells feed principal cells of MNTB and LNTB that drive temporally accurate inhibitory pathways (blue). Octopus cells (thin red) have a temporally accurate onset response. Not shown on this schema, certain multipolar (stellate) cells within AVCN have a temporally accurate onset response (onset-C). Only pathways that feed nuclei on one side of the head are shown here (the same pathways exist on both sides). Pitch extraction could, in principle, occur at any level that receives accurate temporal information. Abbreviations: AC (auditory cortex) MGB (medial geniculate body), IC (inferior colliculus), DNLL, INLL, VNLL (dorsal, intermediate and ventral nuclei of the lateral lemniscus), MSO, LSO (medial and lateral superior olive), MNTB, VNTB, LNTB (medial, ventral and lateral nuclei of the trapezoid body), ALPO, PPO, DMPO, VMPO, DLPO (anteriolateral, posterior, dorsomedial, ventromedial and dorsolateral periolivary nuclei), DCN, PVCN, AVCN (dorsal, posterioventral and anterioventral cochlear nuclei) (from Schwartz 1992; Helfert and Aschoff 1997; Thompson and Schofield 2000).

Tonotopically-organized fields exist at all levels up to thalamus and cortex, reflecting orderly projections from the cochlea, but we argued earlier that pitch is unlikely to emerge from a place-rate representation. Neural activity follows stimulus periodicity up to at most 1000 Hz in IC, 1200 Hz in thalamus or 250 Hz in cortex (Liu et al 2005; Wallace et al 2007). However most neurons have cutoffs well below these limits, and furthermore these ranges cover only part of the range of pitch periodicities. Relaying and processing temporally accurate spike trains entails a cost (in terms of specialized circuitry and metabolism), and it is likely that pitch processing occurs at an early level, possibly as early as the dendritic fields of cochlear nucleus neurons that receive input from the auditory nerve. However the existence of Huggins pitch suggests a locus beyond the level of binaural interaction.

On the assumption that pattern matching is a "high-order" operation, it is sometimes proposed that pattern matching is performed by secondary auditory cortical fields operating on the output of a tonotopically organized primary cortical field. It is more likely that cortical responses elaborate (and possibly recapitulate) pitch-relevant features (or conjunctions of features) extracted at subcortical levels.

It is frustrating that little direct evidence has been found for any particular locus, or model. Signatures of a pitch extractor, expected from pattern matching and autocorrelation alike, are (a) sensitivity to changes in **F0**, and (b) invariance across other stimulus dimensions. The first property is readily observed, but alone it is not sufficient to signal pitch. Evidence for a cortical "pitch centre" has been reported based on cortical recordings in animal or brain imaging in humans (Bendor and Wang 2006; Patterson et al 2002), but methodological issues complicate interpretation of experimental results (McAlpine 2004; Hall and Plack 2008; Nelken et al 2008). A recent report describes single unit responses from presurgical recordings from electrodes implanted in the brains of epileptic patients. Tuning to pure tones (embedded within 3-tone random chords) was extremely narrow, limited only by the resolution of stimulus sampling (1/18th of an octave) (Bitterman

et al 2008). The protocol did not test invariance, and thus we cannot exclude that those responses merely reflect a remarkably selective tonotopy, but the sharp frequency resolution is evocative of a sensitivity to pitch.

Physiologists have obviously looked hard for proof of the various pitch theories mentioned earlier, such as Shamma and Klein's (2000) pattern matching model, Licklider's autocorrelation model (Licklider 1951; Meddis and Hewitt 1990a), or de Cheveigné's (1998) cancellation model. Direct evidence is still lacking, although most of the ingredients (lateral inhibition, within- and cross-channel coincidence, inhibition, etc.) are ubiquitous. Autocorrelation and cancellation models require delays of up to about 30 ms to accommodate a lower limit of pitch of 30 Hz (Pressnitzer et al 2001). Evidence for appropriate delays is fragmentary (Behrend et al 2002; Nayagam et al 2005), although it has been suggested that delays might arise indirectly from cross-channel interaction (de Cheveigné and Pressnitzer 2006). Numerous cells have been found sensitive to stimulus features relevant for pitch, but they usually are also sensitive to irrelevant features, or otherwise disorderly, making them hard to relate to known models. For example, onset cells within the cochlear nucleus fire accurately to each period of certain stimuli (Winter 2005), but their phase sensitivity makes them poor candidates for pitch. Winter et al (2001) and Wiegrebe and Meddis (2004) proposed that arrays of periodicity-tuned chopper cells in the cochlear nucleus are "read out" by coincidence cells in IC. However the best frequencies of those cells cover a limited range (100 to 500 Hz) and their properties are level-dependent at low levels (Winter 2005).

Physiological correlates of pitch processing might escape observation, for example because they are technically hard to measure. It also could be that we *have* observed the correlates of pitch processing, but that they follow a principle that we do not understand. Or it might be the case that pitch is a human trait that is *not* shared by animal models. For example the selectivity of single neuron responses observed by Bitterman et al (2008) within human auditory cortex is not often reported in animal models.

To summarize, the auditory system is equipped with much neural circuitry to process spectral and temporal features relevant for pitch, but exactly where and how this occurs is still a mystery. The answer may come from progress in recording and imaging techniques in animal models and humans, or it may come from theoretical and modeling efforts to make sense of data that are already available.

11 Methods and tools for the study of pitch

Students of pitch are sometimes dismayed, on reading a paper, to find so much devoted to arcane issues of methodology. It is worth understanding what these issues are, if only to filter them out and focus more easily on pitch. It is also important to be able to judge, based on its methodology, whether a study is credible or not.

Introspection once was our only tool to probe the perceptual reality of pitch. Its drawback is that introspection cannot be communicated reliably. Without an external reference to calibrate what one hears, and compare it with others, the researcher is vulnerable to his or her subjectivity, and

disagreements are hard to resolve. Psychophysics provides tools to insure that perceptual phenomena are real and general, and codified in a form that can be shared. Careful control of stimuli and design of task ensure that the quantity probed in the experiment is that intended by the experimenter. Objective procedures and signal detection theory (Green and Swets 1974) allow the performance limits of a subject to be factored from the effects of response bias and criteria. Statistical tests protect us from over-interpreting random quirks in the data, and they can also give some indication about whether patterns observed reflect the idiosyncrasies of the subjects used in the experiment, or instead are of wider validity. These tools help produce results that are reproducible and credible. The downside is that the task (remembering instructions, pushing buttons, etc.) and stimulus repetition may interfere with the process of perception. Phenomena that do not fit the requirements of these tools may be overlooked.

Psychophysics allows strong inferences on mechanisms within the brain, but it is no substitute for direct observation of neural activity. The most detailed observations are made in animal models using invasive techniques, such as the recording of the electrical activity of single or multiple neural units in response to the kind of stimuli that would produce pitch in humans. Other techniques involve measuring local field potentials or optical correlates of neural activity. With a background of knowledge of the brain from a variety of techniques, physiology in animal models gives us the most detailed picture of the neural processes that could be involved in pitch processing (Winter 2005; Tramo et al 2005; Cariani and Delgutte 1996a,b). An obvious drawback is that animals may differ from us in some important way in their experience of pitch, or in their processing of pitch-evoking sounds, or both. It is hard to do psychoacoustics in animals (see chapter by Shofner) and impossible to get them to describe what they heard, so we cannot be sure whether an observed response reflects pitch.

Brain imaging allows observation of brain activity in the species that interests us most: our own. *Structural* magnetic resonance imaging (MRI) has found correlations between the size of anatomical structures and pitch-related abilities (Gaser and Schlaug 2003; Schneider et al 2005). *Functional* magnetic resonance imaging (fMRI) and positron emission tomography (PET) have been used to investigate pitch-related activity within the brain (Griffiths et al 1998; Patterson et al 2002; Warren et al. 2003; Griffiths 2005). Evidence has been found for a "pitch centre" in lateral or anterolateral Heschl's gyrus (Patterson et al 2002; Penagos et al 2004), but this result has recently been questioned (Hall and Plack 2008). The spatial resolution of fMRI (on the order of 1 cm) allows gross localization of neural activity, but its limited temporal resolution (about 10 s) constrains conclusions concerning the sequence of neural events (Griffiths 2005).

Electroencephalography (EEG) and magneto-encephalography (MEG) offer better temporal resolution than fMRI, on the order of 1 ms. The onset response to periodic tones (pure or complex) includes a component (N100m) with a latency close to 100 ms that varies systematically with the period (Forss et al 1993; Stufflebeam et al 1998; Roberts et al 2000; Crottaz-Herbette and Ragot 2000; Lütkenhöner et al 2001; Seither-Preisler et al 2006). However similar onset responses occur for sounds that do not evoke pitch. It is thus imprudent to claim that N100m latency "codes" pitch, or any other stimulus parameter or qualia. Presenting the pitch-evoking

stimulus preceded by a noise-like waveform with similar spectral envelope allows a "pitch onset response" (POR) to be separated from the generic onset response (Krumbholz et al 2003; Gutschalk et al 2004). POR latency and amplitude vary with stimulus period and degree of periodicity, suggesting a pitch-specific response. However similar responses were observed for transitions between stimuli that differ in regularity but do not evoke a pitch (Chait et al 2007, 2008). MEG claims relatively good spatial resolution, and has been used to find evidence for a "tonotopic" or "periodotopic" organization of human auditory cortex (Romani et al 1982; Pantev et al 1988; Langner et al 1997). Results of different studies are unfortunately contradictory. Localization of sources is highly dependent on a single-dipole model that is not sufficiently accurate to allow such fine-grained conclusions (Lütkenhöner 2003; Lütkenhöner et al 2003).

In summary, despite their considerable popularity and authority, non-invasive brain imaging techniques offer only limited insight into pitch perception mechanisms. Issues are limited spatial or temporal resolution, high levels of noise and variability in measured responses, bias towards structures and phenomena that are easy to image, the uncertain relation between the quantities measured (BOLD in fMRI, currents in dendrites of large populations of pyramidal neurons for MEG and EEG) and relevant activity within the brain, and the need for sophisticated models and statistical procedures to make sense of the data.

Invasive recording techniques potentially provide a more detailed picture of human brain activity (Liégeois-Chauvel et al 1994; Lachaux et al 2003; Schönweiser and Zatorre 2008; Schnupp and King 2008; Bitterman 2008). As part of presurgical protocol in epileptic patients, arrays of subdural electrodes are placed on the surface of the cortex (similar to EEG but without the deleterious effect of the high-impedance skull), or depth electrodes are inserted to record both local field potentials and individual neural units within the brain. Proximity to structures of interest, and favorable signal-to-noise ratio, give them an advantage over non-invasive recording techniques, at the expense of severe constraints on the availability of patients and the sampling of brain areas of interest. In common with brain imaging, invasive recording techniques offer only a sparse sampling of the complex activity within the brain.

Models and theories are important tools, indispensable to guide the design of experiments, and stitch their fragmentary results together into a picture that "makes sense" to our understanding. Models of pitch are reviewed by de Cheveigné (2005). Special mention must be made of software models, that allow complex experimental data to be compiled and confronted against theoretical hypotheses. A promising new trend is the use of theoretical neuroscience and machine-learning techniques to bridge the gap between experimental data and high-level functions involving cognition and action. Unfortunately it may be difficult for the student of pitch to judge the validity of theories that require mathematical sophistication, or that are embodied by the lines of a computer program. Modeling, to be useful, requires care to specification (*what* does the model do) and pedagogy (*how* does it work).

Applications such as speech recognition, music processing, or sensory prostheses obviously benefit from our understanding of hearing. They also

contribute to understanding in an important way: by testing the validity of our hypotheses in the context of "real world" tasks.

As mentioned earlier, the arcane methodological details of many studies on pitch may disorient the reader interested in pitch. Complex tone stimuli are often presented without their fundamental component. Originally the aim was to probe effects beyond those expected from a classic "place" explanation, an aim that makes sense within the context of the "missing fundamental" debate (Section 5). That debate has subsided, but excluding the fundamental component is still useful in physiological studies to distinguish between the selectivity to pure tone frequency that is ubiquitous in the auditory system, and sensitivity to pitch. Complex tones may also be stripped of additional low-order harmonics (e.g. below the 10th). The aim here is to remove resolved partials so that the stimuli offer only "temporal" cues, as opposed to spectral cues usable by a pattern-matching mechanism. This precaution is relevant in the context of the "resolvability" debate (Section 7).

Without additional precautions, these efforts may be compromised by nonlinear distortion products that arise within the cochlea. For example, *difference tones* produced by pairs of partials ($f_2 - f_1$, where f_1 and f_2 are partial frequencies) may introduce components at the fundamental and low harmonics (Pressnitzer and Patterson 2001). Likewise, *cubic difference tones* ($2f_1 - f_2$) may introduce components just below the lowest harmonic of a set of high-frequency partials. To mask these distortion products, that behave like rogue stimulus components, noise is added in the frequency region where they occur. The noise may be white (flat spectrum), or pink (power varies as $1/f$), or adjusted for uniform masking or for equal thresholds in each cochlear channel (threshold-equalized noise, TEN, Moore et al 2000). The aim in each case is to mask the distortion products while minimizing any deleterious effect on the stimulus itself.

Stimulus manipulations designed to affect pitch might also affect other perceptual dimensions. To rule out the possibility that a subject uses, for example, a change in loudness instead of pitch as a cue for a task, the stimulus level may be *roved* between trials. Likewise, a change in **F0** may produce physiological responses unrelated to pitch in physiological or brain imaging experiments, and therefore characterizing a genuine pitch effect may require testing over a range of pitch-producing stimuli (Hall and Plack 2008).

In summary, we have many tools at our disposal to explore pitch. Each has "blind spots" that we must understand, and that we may compensate for to some degree by combining them. Advances in tools and methods may induce major leaps in our understanding, as argued earlier by von Békésy and Rosenblith (1948). In particular, progress in the resolution and signal-to-noise ratio of recording and imaging techniques, coupled with careful use of standard behavioral techniques, might lead to a quantum leap in understanding pitch.

12 Conclusion

Pitch is an important quality of sound, the focus of intense inquiry and investigation since antiquity. Pitch is basic to two forms of behavior specific to humans: speech and music. Pitch is usually understood as a one-dimensional percept determined by the period of the stimulus (or its inverse, F_0), and insensitive to changes along other stimulus dimensions. However its complex role within music involves harmonic and melodic effects that go beyond this simple one-dimensional model.

There is still debate as to where, and how, pitch is extracted within the auditory system. Helmholtz's influential idea that pitch is determined by the locus of maximal vibration within the cochlea is no longer accepted. Rather, it is more likely that pitch is extracted within the auditory nervous system on the basis of temporal patterns transduced from acoustic vibrations within the cochlea. The site of pitch extraction is unknown, but probably relatively peripheral within the lower auditory brainstem or midbrain where temporally accurate neural information is available. Multiple neural substrates appear to be specialized for time, but the shape of many of their responses to sound are complex and difficult to relate to existing models of pitch.

According to the pattern-matching hypothesis, the frequencies of individual partials are estimated and matched against a set of internal harmonic templates. Partial frequencies could be estimated from neural temporal patterns within neural channels within which they are isolated by cochlear filtering, and possibly also from temporal patterns between those channels. As such, pitch perception might be dependent on both the selectivity and the phase properties of a healthy cochlea. According to the autocorrelation hypothesis, the period is instead determined directly from the temporal pattern of nerve activity transduced by the cochlea, by a neural circuit involving an array of delays (or one tunable delay) and coincidence-detecting neurons. According to that hypothesis cochlear selectivity would not be directly involved in period estimation, but it might be useful to isolate sources within noise and facilitate perception of their pitch. Alternatively, cochlear mechanics might contribute to create the necessary delays, which would then also depend on the healthy condition of the cochlea. Physiological and psychophysical investigation have failed to rule decisively in favour of either hypothesis, and it may be the case that pitch is extracted according to a mechanism that is yet to be discovered.

Investigation tools for pitch include psychophysics, electrophysiology in animal models, brain imaging in humans, and theoretical and engineering approaches to solve similar problems in artificial systems. The study of pitch requires special care to methodological questions (e.g. combination tones), that sometimes obscure the pitch-related issues and make the literature hard to read for the newcomer. Once these issues are understood, pitch perception unfolds itself as a fascinating field where there is still much to be learned.

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