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The Neural Basis of Individual Holistic and Spectral Sound Perception

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With respect to enormous inter-individual differences in sound perception, this article aims to review the research background of the neural basis of individual sound perception. Principally, two basic listening types can be distinguished: 'holistic' or 'synthetic' listeners recognize the sound as a whole, and appreciate its pitch and timbre as characteristic qualities of the entire sound; and 'spectral' or 'analytical' listeners break up the sound into its harmonic constituents, at the expense of timbral qualities of the sound as a whole. In-between these two extreme listening modes, intermediate listeners perceive holistic and spectral cues simultaneously to varying degrees (auditory ambiguity). Several recent neurological investigations have pinpointed these perceptual differences to neuroanatomical and neurophysiological measures of the auditory cortex. Furthermore, it has been shown that individual auditory perception bias corresponds to musical instrument preference and musical performance style. Multimodal research findings point towards an individual 'fingerprint' of auditory cortex and perception profiles; however, whether these properties are shaped by intense training or rather reflect innate, genetically determined predisposition remains a matter of unresolved debate.

Keywords: Interindividual Variability; Sound Perception; Pitch; Timbre; Heschl's Gyrus

Introduction

Harmonic complex tones are composites of at least two sinusoidal components whose frequencies are integer multiples of the fundamental frequency (Scharf & Houtsma, 1986). Most natural sounds such as musical instruments or voice are composed of one fundamental and multiple integer harmonics (Figure 1C) including distinct subgroups of few adjacent harmonics that form the characteristic sound formants of the respective musical instrument. Such subgroups of harmonics with two, three or four adjacent partials play an important role in psychophysical (Moore, 1997; Preisler, 1993; Seither-Preisler et al., 2007; Terhardt, 1974) and neurophysiological research (Pantev et al., 1989; Schneider et al., 2005a; Zatorre, 1988; Zatorre & Belin, 2001) of sound perception. Remarkably, enormous inter-individual differences

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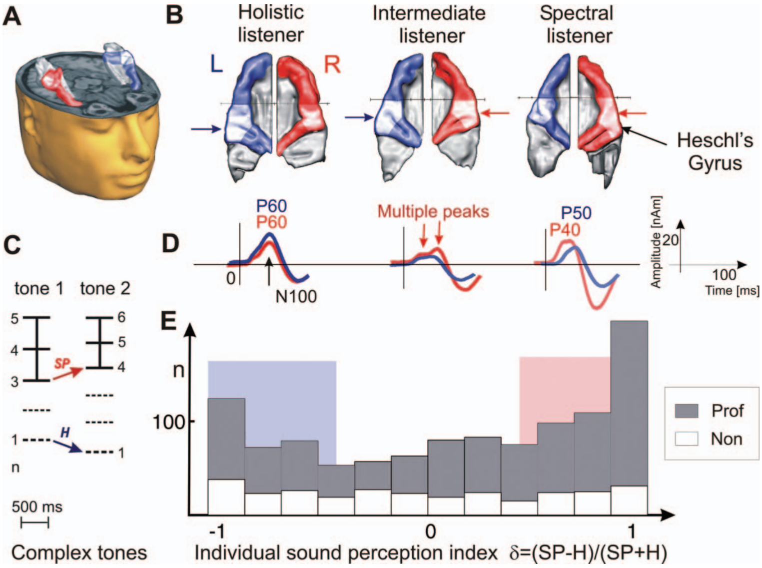

Figure 1 Individual and average sound perception preference. (A, B) Top view of segmented auditory cortices illustrating the anatomy of Heschl's gyrus (see issue cover: left side is blue-coloured and right side is red-coloured). (C) Experimental design: Participants are required to state the dominant direction of pitch shift between tone pairs. Solid lines represent the harmonics of the test tones, dashed lines the harmonics that are not physically present (e.g., the missing fundamental, indicated as number one). (D) Characteristic electrophysiological responses of the primary auditory cortex of the first 100 ms after tone onset. (E) Averaged over the middle and low frequency ranges ($f \leq 1.5$ kHz), professionals show a bimodal distribution (grey bars), non-professionals a uniform distribution (white bars). The separation of extreme fundamental, intermediate and extreme spectral listeners is labelled by blue-, white- and red-coloured areas in the background, respectively.

of sound perception have been observed in musicians and non-musicians alike (De Boer, 1976; Houtsma & Fleuren, 1991; Laguitton et al., 1998; Renken et al., 2004; Rousseau et al., 1996; Schneider et al., 2005a; Seither-Preisler et al., 2007, 2008; Singh & Hirsh, 1992; Smoorenburg, 1970; Terhardt, 1974). Principally, two extreme listening modes can be distinguished: 'holistic' listeners perceive the sound with its pitch and timbre as a whole with emphasis on the fundamental tone; and 'spectral' listeners decompose the sound into its single harmonic constituents. By perceiving a collective spectral chord of adjacent harmonics, spectral listeners may therefore loose the timbral qualities of the sound as a whole (De Boer, 1976; Helmholtz, 1863; Schneider et al., 2005b; Terhardt, 1974). (Please refer to the Appendix for terminology).

Such subjective aspects were described earlier by the German physician and physicist Hermann von Helmholtz who coined the terms 'synthetical mode', based on holistic sound perception (harmonics 'fuse into the whole mass of musical sound'), and 'analytical mode', based on the separate perception of single harmonics. The physicist August Seebeck was the first who demonstrated that the fundamental pitch can even be perceived when it is physically absent (Seebeck, 1843). In particular he observed that a group of higher harmonics ($n > 10$) was collectively heard as a solitary sharp fundamental pitch. This type of percept was historically labelled 'residue pitch' (Schouten, 1940). Shortly thereafter, Georg Ohm (1843) formulated his famous acoustic law, which states that a sound is solely perceived by the chord of constituent pure harmonic tones (disregarding a potential missing fundamental tone). This idea of musical sound perception being determined only by its partials was supported by Helmholtz as well (Helmholtz, 1863). Nowadays, it might be hypothesized that the historical dispute between Ohm and Seebeck on the existence of the missing fundamental might have been caused by their individual difference of sound perception (Ohm, 1843; Seebeck, 1843): we speculate that Seebeck might have been a typical 'holistic listener' with strong fundamental tone perception, whereas Ohm and Helmholtz were most likely 'spectral listeners', for whom the missing fundamental of the stimuli in question simply might not have been audible.

Approximately 100 years later, technical developments and the possibility to actually generate complex harmonic tones with a clearly defined number of harmonics allowed for the systematic investigation of the cross-link between individual sound perception and physical sound properties (Figure 1). It has been observed that missing fundamental pitch sensations can be evoked with very a limited spectra of five (De Boer, 1956), three (Ritsma, 1962; Schouten, 1962) or only two adjacent harmonics (Smoorenburg, 1970). Furthermore, even the dichotic presentation of two-component stimuli, where only one component is presented to each ear, may induce the perception of a missing fundamental (Houtsma, 1979; Houtsma & Goldstein, 1972). Later, Houtsma (1984) and Zwicker and Fastl (1999) investigated the salience of fundamental pitch sensations as a function of different acoustic parameters and found a perceptual continuum from clear to scarcely audible fundamental pitch. They found that fundamental pitch salience was strongest for low center frequencies and low average harmonic numbers (Fastl, 1998; Seither-Preisler et al., 2003, 2006).

Individual Sound Perception

In order to quantify the remarkable perceptual differences psychoacoustically, Schneider et al. (2005b) performed a novel pitch perception test following a traditional psychometric test paradigm based on tone pairs of harmonic complex tones (Houtsma & Smurzynski, 1990; Laguitton et al., 1998; Smoorenburg, 1970). Participants were asked to identify the dominant direction of pitch shift in a sample set of 144 tone pairs (Figure 1C). The spectral components of each tone pair were composed of the following elements: eight different harmonic numbers (ranging from 2 to 15); six different highest component frequencies (294, 523, 932, 1661, 2960 and 5274 Hz); and three different numbers of components ($N = 2$, 3 and 4).

Importantly, the highest component frequency was kept constant between tones of one pair to ensure timbre consistency. For each test participant, a psychometric asymmetry coefficient was derived by recording the number of holistic (*H*; formerly referred to as 'fundamental') and spectral (*SP)* classifications, computing an 'index of sound perception preference' according to the formula $\delta = (SP - H) / (SP + H)$. Within a large group of 334 professional musicians, 75 amateurs and 54 non-musicians there was a broad and even distribution, with peaks at either extreme (Figure 1E). Accordingly, subjects were categorized as either pure 'holistic listeners', who exclusively perceived the missing fundamental throughout the whole range; pure 'spectral listeners', who were utterly incapable of hearing a missing fundamental; or intermediate listeners, who were able to perceive both the holistic and spectral cues depending on the frequency range. In some cases, intermediate listeners perceived stimuli ambiguously in form of a 'conflicting pitch'.

Auditory Ambiguity

In order to further investigate such auditory ambiguity, Seither-Preisler et al. (2007) composed an 'Auditory Ambiguity Test' (AAT) to test for the relative predominance of holistic and spectral listening mode. In the AAT, missing fundamental frequencies form melodic intervals (major second, major third, fourth, fifth, major sixth) and the upper spectral frequencies are not fixed. This test revealed that professional musicians showed very consistent behavior towards auditory ambiguities, whereas responses of non-musicians were toggling and highly inconsistent in repeated measures with no clear identification of holistic or spectral listeners. In order to investigate potential learning-induced changes of auditory perception, Seither-Preisler et al. (2008) conducted a follow-up-study in which non-musicians with auditory ambiguity were trained by performing repetitive AAT measures for two months. Interestingly, sound perception gradually changed in favor of the missing fundamental pitch. This finding is remarkable as subjects were neither informed about the ambiguous nature of the stimuli, nor did they receive any feedback on their performance, and they were completely unaware of the gradual perceptual changes they underwent. These findings suggest that subjects with auditory ambiguity might be sensitive to plastic changes in pitch perception.

Historically, auditory ambiguities have been repeatedly reported by numerous musicians and scientists. Already Helmholtz (1863) noted that octave errors may occur frequently to non-musicians and to professional musicians alike. Various composers, such as Arnold Schönberg (1911) have also described the similarity of tones and their octaves. Patterson (1973) outlined that the subjective pitch perception of harmonic complex sounds with few harmonics may correspond to either the fundamental frequency or the octave-shifted second harmonic. Similarly, Terhardt (1972) found differences of an octave or a fifth between the nominal fundamental pitch and the subject's actual percept. This uncertainty appears to be related to a well-known musical phenomenon: the 'octave equivalence'.

Fundamental Pitch, Chroma and Timbre

Musical sound is mainly determined by fundamental pitch and the timbral qualities of the spectral harmonics. These elements are classically defined as independent parameters (ANSI, 1960). However, there is evidence for a reciprocal dependency, such as instrument-specific timbre changes across the register of musical instruments (Marozeau et al., 2002). Early fundamental investigations on sound perception already suggested that sound qualities such as pitch, chroma and timbre may be perceived in varying ways depending on where the listener's attention is focused (De Boer, 1976; Helmholtz, 1863; Terhardt, 1974). Modern research has lead to a modification of this viewpoint; attention may be shifted intentionally within a given range of the individual listening mode. However, the continuum in which the listener may shift his or her attention is constrained by the individual sound perception mode—namely, holistic listeners perceive pitch, chroma and timbre as qualities of the entire sound, whereas spectral listeners decompose the sound into its spectral components.

The composer Arnold Schönberg illustrated his subjective impression of the dependencies of sound qualities:

> I cannot readily admit that there is such a difference, as is usually expressed, between timbre and pitch. It is my opinion that the sound becomes noticeable through its timbre and one of its dimensions is pitch. In other words: the larger realm is the timbre, whereas the pitch is one of the smaller provinces. The pitch is nothing but timbre measured in one direction. (Schönberg, 1911)

Neural Correlates of Holistic and Spectral Sound Perception

Individual differences in sound perception and auditory ability have been found to correlate with individual neuroanatomical and functional markers of auditory brain areas (Schneider, 2002, 2005b, 2009). Particularly, the so-called 'Heschl's gyrus' (HG, named after the Vienna anatomist Richard Ladislaus Heschl), which hosts most parts of the primary and secondary auditory cortex, was found to harbor important areas for music and sound processing. Neuroimaging studies revealed that the 'pitch extraction centers' are hosted in the lateral parts of HG (Patterson et al., 2002; Penagos et al., 2004; Warren et al., 2003), which are highlighted in Figure 1B. The left auditory cortex is specialized for rapid temporal and the right for spectral processing (Boemio et al., 2005; Hyde et al., 2008; Liegeois-Chauvel et al., 2001; Schönwiesner et al., 2005; Zatorre & Belin, 2001; Zatorre & Gandour, 2008).

There are enormous inter-individual differences in terms of shape, gyration, size and number of duplications of HG. Interestingly, non-musicians usually have a small, single HG, whereas professional musicians often show 100% volume increase and one or more HG duplications. As an illustration, Figure 1A depicts the anatomical position and structure of the right and the left auditory cortex of a professional singer. Figure 1B presents the top view of the right and left HG of three professional musicians with different listening modes. Note that HG may occur either in form of a single crescent-, banana- or boomerang-shaped gryus, or in the form of multiple duplications and/or bifurcations on one or both sides, depending on the predominant listening mode. More than seventy years ago, the anatomist Pfeifer (1936) argued, that 'if there is any relation between morphology and function, the sense of hearing must show the most pronounced variations' (see also Steinmetz et al., 1989). Indeed, Schneider et al. (2002, 2005b) found for the first time that individual sound perception is reflected by shape and predominance of the right or left Heschl's gyrus. In bilateral comparison, holistic listeners (previously referred to as 'fundamental pitch listeners') exhibited increased gray matter volume and greater activity in the left HG. In contrast, dominant spectral listeners exhibited larger right HG volumes (Figure 1B).

Consistently, characteristic auditory responses could be observed in each hemisphere according to the predominant listening mode. First, auditory responses of noise bands with either varying temporal rate or number of spectral components assessed by functional magnetic resonance imaging (fMRI) revealed larger sensitivity to rapid acoustic changes in left HG and preferential processing of complex spectral information in right HG (Schönwiesner et al., 2005; Warrier et al., 2009). This substantiates the so-called 'spectrotemporal trade-off' model of acoustic processing, which states that 'functional lateralization of acoustic encoding contributes to the leftward-lateralization elements of language and the rightward-lateralization elements of music' (Zatorre et al., 2002).

Second, the auditory evoked fields in the pitch-sensitive areas of HG, as measured by magnetoencephalography (MEG) in response to both harmonic complex tones and musical instrument sounds, showed a characteristic timing and sensitivity of the cortical pitch areas within a specific early time range of 30 to 70 ms after tone onset (Schneider et al., 2005a, 2005b). Auditory responses of spectral listeners started approximately 5–25 ms earlier on the right hemisphere, often presenting with multiple response peaks. Responses of holistic listeners, on the other hand, showed synchronous and slightly decelerated peaks in both auditory cortex (Figure 1D). Intermediate listeners presented with ambiguous patterns of two separate peaks in the right auditory cortex and a plateau-shaped pattern of the left auditory cortex. As the auditory input was constant across all subjects, these characteristic individual responses at the primary auditory processing level could not be explained by peripheral latency shifts that are induced by frequency-dependent travelling wave delays (Patterson, 1994). Rather, they are exclusively based on the subjective, perceptual domain.

Furthermore, several recent MEG studies provided additional evidence for early cortical processing of holistic and spectral pitch—namely in response to harmonic complex sounds with a spectral center of gravity at 1.8 kHz, Monahan et al. (2008) found early auditory restoration of a holistic sound percept at the level of the prominent late auditory evoked negative 'N100 response' occurring at 100 ms after tone onset. In response to incomplete complex tones consisting of the 4th to 11th harmonics, Pantev et al. (1996) found that the center of the auditory evoked N100 activation within the cortical tonotopic map corresponded to the location of the perceived pitch (and not to the locations that are activated when the single frequency constituents are presented). The combined MEG-psychoacoustic study of Chait et al. (2006) demonstrated that the 'pitch onset response' at 150 ms in response to binaurally created pitches reflects central pitch mechanisms, in agreement with models postulating a single, central pitch extractor. In a further MEG study, Pantev et al. (2001) reported that highly skilled musicians (i.e., violinists and trumpeters) exhibited enhanced auditory cortical representations for musical timbres associated with their instrument, compared to timbres associated with instruments on which they have not been trained. Taken together, these studies suggest that individual differences in sound perception are reflected both anatomically and functionally already at the level of the primary and secondary auditory cortex.

Individual Preference of Musical Instruments and Performance Styles

Recent neuroimaging studies on spectrotemporal processing of auditory brain areas suggest that differences in individual morphology and function of auditory cortex might be a neural predictor for musical instrument preference and musical performance style. To quantify in more in detail the relationship between sound perception and musical instrument preference, Schneider et al. (2005a) studied the psychoacoustic profile of 463 musicians with respect to their main music instrument, their musical preferences and their musical instrument preferences. The degree of holistic versus spectral listening mode was averaged over instrumental groups and the psychometric results were analyzed for different instrument families. Percussionists showed the most pronounced holistic sound percept, followed by trumpeters, guitarists and flutists. On the other hand, players of lower-pitched instruments (bassoon, double bass, organ or basses and altos in a choir) were found to show the most pronounced spectral sound percept.

Considering that the left auditory cortex is sensitive to short time scales (25–50 ms), and the right auditory cortex to slower timescales (200–300 ms) (Boemio et al., 2005), it is perhaps unsurprising that musicians with a left hemispheric dominance were found to have a preference for percussive and higher pitched musical instruments such as drums, trumpet, cembalo or plucked instruments (e.g., the guitar), which all have a sharp tone onset without characteristic formant regions in the spectrum (Gieseler et al., 1985; Schneider et al., 2005a). In the same way, musicians with a right hemispheric dominance and dominant spectral listening mode preferred melodic and overtone-rich instruments such as organ, lower-pitched wood instruments, strings or voice, because the sound of these instruments is characterized by sustained sound fields, slower attack times and salient spectral formant regions. Some subgroups, such as pianists, violinists or flutists, showed a broad distribution of sound perception, indicating an additional influence of musical performance preference. Regarding the distribution of the 106 pianists, about 65% were holistic listeners and 35% spectral listeners.

Further analysis of the instrumentalists musical background and performance style revealed that pianists with holistic sound perception preferred to perform more with virtuosity and enjoyed playing complex rhythmic patterns, whereas pianists with dominant spectral sound perception preferred slower music and concentrated more to control for timbre changes or melodic aspects of the music. Therefore, classical pianists were usually holistic listeners and conjure the typical piano sound of a Beethoven sonata or a Liszt etude by a strong control of the tone attack with respect to timing, sharpness and impulsiveness, whereas jazz pianists often were strong spectral listeners. It might be an explanation that for the understanding of jazz performance and composition, to conceive the jazz chord function of lower intervals (3rd, 5th and 7th) or the characteristic timbre of upper intervals or extensions (9th, 11th or 13th) of the 'voicings', spectral pitch decoding might be advantageous.

Furthermore, almost all organists of the study were strong spectral listeners with affinity to baroque music (J. S. Bach), in particular to historically informed performance, expressive romantic (J. Brahms, C. Franck) and modal style (J. Alain, O. Messiaen). The variety of timbral qualities of the different organ pipes and the expansion of formant regions in the space of a large cathedral may be an adequate challenge for spectral listeners. Moreover, there appeared to be remarkable perceptual group differences between complete symphony orchestras or conservatories. Orchestra musicians from Mannheim, Germany, (Nationaltheater Mannheim) were predominantly fundamental pitch listeners, whereas orchestra musicians from Liverpool (Royal Liverpool Philharmonic Orchestra) were almost exclusively spectral listeners (Schneider et al., 2005a). Most notably, the interpretation of the same orchestral work (e.g., J. Strauss, *Alpensinfonie*, op. 64) differed in clear accentuation of synchronized timing among the fundamental pitch listeners (Mannheim) and a strong balance and sensitivity for timbre in the group of spectral listeners (RLPO).

Such co-dependence of individual sound perception and music preference was not only observed in professional musicians, but also in non-musicians and amateurs. In a large-scale online survey, data of 5,700 subjects were collected with respect to musical training, instrumental preference and favorite music in conjunction with a short version of the pitch perception test (including twelve representatives out of 144 tone pairs). Again, in total, an even distribution of pitch perception was found and there were no significant age or gender effects. However, there were significant differences in subgroups of subjects who favored specific music: hard rock fans were mainly holistic listeners (mean delta of –0.46 ($n = 208$) in the range of –1 to +1) (Figure 1E), whereas subjects who stated opera or jazz as favorite music were predominantly spectral listeners (mean delta of opera fans +0.25 ($n = 192$), mean delta of jazz fans +0.51 ($n = 357$) (Tantschinez, 2006).

Brain activation of motor co-representations can occur in trained pianists not only by listening to piano tones, but also by observing a pianist's finger movements while watching a video, thus impressively demonstrating a mirror system of auditory-motor synchronization (Altenmüller, 2008). These findings suggest that an individual profile of sound perception or mental representation of music may be accompanied by a characteristic interaction of multimodal sensory and auditory-motor interactions (Chen et al., 2008; Zatorre et al., 2007). For spectral and holistic listeners, these training-dependent adaptations of motor control functions such as timing, sequencing and spatial organisation of movements may be strongly different and might be a consequence of the individual sound perception profile.

Neuroplasticity

Whether the observed inter-individual differences and their relation to musical competence are due to genetic factors or to training-induced plasticity still remains a matter of unresolved controversy. The hypothesis of long-term audio- and neuroplasticity through instrumental training is undoubtedly plausible (Pantev et al., 2001; Sluming et al., 2002), especially since neuroplastic changes have been observed in other areas such as increased grey matter in the hippocampus (a crucial area of the limbic system controlling long-term memory and spatial navigation) in London taxi drivers (Maguire et al., 2000) or subsequent to juggling training (Draganski et al., 2004). However, other neuroimaging studies (e.g., on absolute pitch perception) point towards a considerable influence of genetic factors with respect to brain structures (Zatorre, 2003).

Gougoux et al. (2004) investigated auditory long-term plasticity in blind and sighted subjects at the cortical level. They found that early-blind subjects were significantly better at determining the direction of pitch changes than both sighted and late-blind subjects. Using a voxel-based morphometry approach (VBM)—a neuroimaging method that allows for group-wise comparison of differences in brain volume—it was reported that age-associated gray matter loss in the motor language area of the brain was reduced in orchestral musicians as opposed to non-musical controls (Sluming et al., 2002). Furthermore, the left auditory cortex of musicians was found to be increased (Gaab et al., 2006; Gaser & Schlaug, 2003), which the authors interpreted as a training-induced neuroplasticity effect. However, the high inter-individual anatomical variability of the HG with respect to gyration and angulation (Steinmetz et al., 1989) may constitute a disadvantage for VBM approaches because inter-individual anatomical variability is likely to be obscured in group studies (Tisserand et al., 2004). Thus, individual reconstructions of cortical subareas are indispensable to revealing the neural basis of individual music aptitude profiles.

Summary and Outlook

Our review emphasizes that the perception of musical sound shows high individual variability. Two groups of extreme listening modes can be distinguished, with spectral listeners decomposing the sound into its single harmonic constituents and holistic listeners perceiving the sound as a whole with emphasis on the fundamental tone. Musicians with holistic listening mode and associated leftward auditory dominance were found to prefer percussive and higher pitched musical instruments, such as drums, trumpet, cembalo or plucked instruments, which all have a sharp tone onset without characteristic formant regions in the spectrum. In contrast, musicians with dominant spectral listening mode and associated right-hemispheric dominance tend to prefer non-percussive, melodic and overtone-rich instruments such as the organ, lower-pitched wood instruments, strings or voice.

A detailed analysis of individual sound perception profiles with timbre dependent input variables (e.g., frequency, height and number of harmonics) may shed light on the specific relevance of characteristic formant regions of the respective music instruments. The strong perceptual and morphometric differences between the orchestra musicians of Liverpool (RLPO) and Mannheim (Nationaltheater) indicate that further cultural aspects and the tradition of interpretation and performance are important factors, which may be the consequence of sound perception preference. Further long-term studies on training-naïve individuals before and after musical education are required to clarify whether the observed differences may either be related to a stable individual musical aptitude profile based on genetic disposition, or rather represent the result of audio- and neuroplastic changes caused by intense musical training.

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Appendix. Terminology (alphabetical).

Complex tone	Sound consisting of several harmonic components
Formant	Peak in the frequency spectrum of a sound caused by acoustic resonance (Tietze, 1994)
Fundamental	Largest common devisor of the frequencies of a complex tone; the fundamental may be physically present or not
Fundamental pitch	Perceived pitch of the (missing) fundamental of a complex tone (Helmholtz, 1863; Terhardt, 1974)
Harmonics/components	Physical part tones (pure tones) of a harmonic complex tone. All harmonics are integer multiplies of a low fundamental frequency
Holistic listener	Focusing on the sound as a whole, and appreciating its pitch and timbre as a characteristic quality of the entire sound
Missing fundamental	Fundamental of a complex tone that is physically absent
Octave-independent fundamental	Fundamental of a complex tone characterized only by *tone chroma*, but not by *tone height* (Patterson, 1990)
Pitch strength	Psychoacoustic magnitude describing how strongly the pitch of a sound can be perceived (Fastl, 1998)
Spectral listener	Break up the sound into constituent sounds, perceive a collective spectral chord of adjacent harmonics and loosen the timbral qualities of the sound as a whole
Voicing	Instrumentation and vertical spacing and ordering of the pitches in a chord