

NEURAL TRANSFORMATION OF DISSONANT INTERVALS IN THE AUDITORY BRAINSTEM

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ACOUSTIC PERIODICITY IS AN IMPORTANT FACTOR for discriminating consonant and dissonant intervals. While previous studies have found that the periodicity of musical intervals is temporally encoded by neural phase locking throughout the auditory system, how the nonlinearities of the auditory pathway influence the encoding of periodicity and how this effect is related to sensory consonance has been underexplored. By measuring human auditory brainstem responses (ABRs) to four diotically presented musical intervals with increasing degrees of dissonance, this study seeks to explicate how the subcortical auditory system transforms the neural representation of acoustic periodicity for consonant versus dissonant intervals. ABRs faithfully reflect neural activity in the brainstem synchronized to the stimulus while also capturing nonlinear aspects of auditory processing. Results show that for the most dissonant interval, which has a less periodic stimulus waveform than the most consonant interval, the aperiodicity of the stimulus is intensified in the subcortical response. The decreased periodicity of dissonant intervals is related to a larger number of nonlinearities (i.e., distortion products) in the response spectrum. Our findings suggest that the auditory system transforms the periodicity of dissonant intervals resulting in consonant and dissonant intervals becoming more distinct in the neural code than if they were to be processed by a linear auditory system.

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MUSICAL INTERVALS WITH SIMPLE FREQUENCY ratios such as 1:2 and 2:3 are judged to be more consonant, pleasant, or harmonious than those with complex frequency ratios (Plomp & Levelt, 1965). The perception of consonance is considered a universal phenomenon that is culturally invariant and independent of music training (Butler & Daston, 1968). As evidence of this universality, a recent study found that even an infant chimpanzee as young as five months of age discriminates between consonant and dissonant sounds (Sugimoto et al., 2010). In addition, birds, monkeys, and human infants differentiate consonance and dissonance (Trainor & Heinmiller, 1998), which further speaks to the ubiquity of this sensory phenomenon.

To explain sensory consonance — defined as the perception of consonance induced by an isolated musical interval without musical context — numerous theories have been proposed. One prominent contemporary account proposes that sensory consonance and dissonance are attributed to two acoustic variables, namely beating and harmonicity (McDermott & Oxenham, 2008). Intervals with complex ratios have spectral components that are close but not identical in frequency. These neighboring components interfere with each other and produce amplitude modulations in the envelope of the sound. Helmholtz (1877/1954) proposed that these amplitude modulations (beating) evoke the perception of roughness, making certain intervals sound dissonant. In contrast, two tones with simple frequency ratios have common spectral components and do not interact to create roughness, giving rise to sensory consonance. Another modern account of consonance, which originates from pitch-based theories (DeWitt & Crowder, 1987; Green & Butler, 2002; Lipps, 1905; Schneider, 1997), considers the harmonicity of the spectral components contained in musical intervals. Harmonicity refers to the relationships among frequencies, specifically whether the sound contains frequencies that are integer multiples of a given fundamental frequency (Gill & Purves, 2009; Griffiths, Micheyl, & Overath, 2012; McDermott, Lehr, & Oxenham, 2010). For intervals with

small-integer ratios, spectral components with strong harmonicity constitute multiples of a common base note (subharmonic) and produce highly periodic waveforms. In fact, the degree of consonance of a musical interval is predicted by its spectral similarity to a harmonic series (Gill & Purves, 2009) and the periodicity computed from the frequency ratio of the musical interval (Stolzenburg, 2013).

Neural correlates of roughness and harmonicity have been identified. The roughness of dissonant intervals is reflected in the activity recorded from cat auditory nerve fibers (Tramo, Cariani, Delgutte, & Braidia, 2001), cat midbrain, inferior colliculus (IC) (McKinney, Tramo, & Delgutte, 2001), chinchilla IC (Sinex & Li, 2007), and primary auditory cortex of human and macaque (Fishman et al., 2001; Steinschneider & Fishman, 2010) in the form of phase locking to amplitude envelope fluctuations. The neural underpinnings of harmonicity have also been observed in the neural discharge patterns of cat auditory nerve fibers (Tramo et al., 2001) and IC (McKinney et al., 2001). Together these studies show that consonant intervals, compared to dissonant intervals, generate more regular and periodic neural phase locking.

The universality of sensory consonance may be an emergent property of the nervous system. Indeed, theoretical models based on the phase locking of auditory nerve and midbrain (i.e., IC) suggest that a neural periodicity detection mechanism may form the basis of consonance and dissonance (Langner, 1997). This proposition is supported by a concordance between the predictions of theoretical models and actual perceptual consonance judgments (Cariani, 2004; Ebeling, 2008). Empirical studies have also found that phase locked neural activity in the human auditory brainstem reflects the perceptual ordering of consonance (Bidelman & Krishnan, 2009; Bones, Hopkins, Krishnan, & Plack, 2014). Moreover, the physical differences in the periodicity of consonant versus dissonant intervals are faithfully preserved in the auditory system by higher neural synchrony to consonant than dissonant intervals (Fishman et al., 2001; McKinney et al., 2001; Tramo et al., 2001). These findings raise the question, does the auditory system just mirror the acoustic features of the musical interval or modulate them in a certain way? Our previous study (Lee, Skoe, Kraus, & Ashley, 2009) found that the human auditory brainstem response (ABRs) to musical interval includes additional frequency components that do not exist in the stimulus, which are distortion products (DPs) generated by the nonlinear behavior of the auditory system. This result indicates that the auditory system transforms the incoming signal in a nonlinear way. If so, then, what is the role

of auditory nonlinearities in sensory consonance? Neural oscillator models based on the nonlinear synchronization of neurons to musical intervals have been developed (Heffernan & Longtin, 2009; Large, 2010; Shapira Lots & Stone, 2008; Ushakov, Dubkov, & Spagnolo, 2010), but there has been no empirical verification of these models. Our previous study (Lee et al., 2009) provided evidence for nonlinear transformation of musical intervals in the ABR and the data were in line with the prediction of a recent neural oscillator model (Lerud, Almonte, Kim, & Large, 2014); however due to the limited stimulus set (two intervals: major 6th and minor 7th), differences between consonant and dissonant intervals could not be extensively evaluated. By expanding the stimulus set to include intervals with higher degrees of consonance and dissonance (perfect 5th and minor 2nd, respectively), this study aims to compare the subcortical representation of consonant and dissonant intervals. Specifically, by comparing the periodicity of each stimulus and response, we investigate the different manners in which auditory nonlinearities transform consonant versus dissonant intervals. To examine how the neural transformation of the stimulus periodicity is related to DPs, we also analyze and compare the response spectra of consonant and dissonant intervals in our stimulus set. All experimental and data collection procedures followed our previous study (Lee et al., 2009).

Method

SUBJECTS

Ten musically trained adults (7 females and 3 males; mean age 26.5 years, $SD = 3.47$ years) participated in this study. All subjects had normal audiological and neurological function (self-report), had normal click-evoked ABR latencies, and binaural audiometric air-conduction thresholds at or below 20 dB HL for octaves from 125 to 4,000 Hz. Subjects completed a questionnaire that assessed their musical experience in terms of beginning age, length, and type of performance experience. Table 1 provides an overview of the music-specific biographical attributes of participants. In our previous study (Lee et al., 2009), we found differences in how musicians and nonmusicians represented DPs, with musicians showing more robust responses to DP frequencies. Thus, to obtain data containing clear DPs, we limited subject recruitment to professional or amateur musicians who had more than 6 years of instrumental training ($M = 15.1$ years, $SD = 4.51$ years). Informed consent was obtained from all subjects. The Institutional Review Board of Northwestern University approved this research.

TABLE 1. Biographical Attributes of the Participants

Participants	Age	Sex	Instrument played	Age of training commencement	Years of music training	Currently playing
1	30	Female	Piano	4	15	N
2	27	Female	Piano	6	17	N
3	24	Female	Piano	3	15	Y
4	24	Female	Violin/Voice	7	6	N
5	28	Male	Violin	9	9	Y
6	33	Female	Piano	3	21	N
7	24	Male	Piano	7	16	N
8	22	Female	Violin/Piano	3	18	Y
9	24	Female	Piano	5	19	Y
10	29	Male	Trombone/Piano	9	15	Y

TABLE 2. Fundamental Frequencies and Their Ratios for the Four Musical Intervals

Interval name	f ₀ (Hz)	Actual ratio	Equal temperament ratio	Nearest just ratio	Approximate dyad f ₀ (Hz)
Perfect 5 th	166, 110	1.51	1.50	3:2	166/3 = 55.3
Major 6 th	166, 99	1.68	1.68	5:3	166/5 = 33.2
minor 7 th	166, 93	1.78	1.78	16:9	166/9 = 18.6
minor 2 nd	166, 156	1.06	1.06	16:15	166/16 = 10.4

STIMULI

Four musical intervals with varying degrees of consonance were presented diotically: perfect 5th (P5), major 6th (M6), minor 7th (m7), and minor 2nd (m2). According to music theory and experimental data (Butler & Daston, 1968; Kameoka & Kuriyagawa, 1969), P5 is the most consonant among these four intervals, followed by M6 and m7, with m2 being the most dissonant. For all four intervals, the upper tone was E3 (166 Hz). The lower tones were A2 (110 Hz) for P5, G2 (99 Hz) for M6, F#2 (93 Hz) for m7, and D#3 (156 Hz) for m2. In all cases, the ratio of two fundamental frequencies deviates only slightly from an exact integer multiple ratio, 2:3 for P5, 3:5 for M6, 16:9 for m7, and 15:16 for m2 (Table 2). The intervals were 400 ms in duration, with the harmonically complex timbre of an electric piano (Fender Rhodes recorded from a digital synthesizer). Each tone contained a fundamental frequency (f_0) as well as multiple harmonics of the f_0 . The relative amplitudes of the f_0 s and harmonics are presented in Table 3. The M6 and m7 stimuli were used in our previous study (Lee et al., 2009). Since four of the ten subjects in our data pool participated in our previous study, their data for M6 and m7 were taken from this existing dataset.

PROCEDURE

All experimental and data collection procedures followed our previous study (Lee et al., 2009). Four musical intervals were presented in separate testing blocks with

block order varied across subjects. The intervals were binaurally (diotically) presented through insert earphones (ER3; Etymotic Research) at an intensity of ~70 dB sound pressure level (Neuroscan Stim; Compumedics) in alternating polarities. Interstimulus interval ranged from 90 to 100 ms. During testing, subjects watched a muted movie of their choice with subtitles in accordance with standardized testing procedures for ABRs (Skoe & Kraus, 2010a).

Auditory brainstem responses were collected at a sampling rate of 20kHz using a PC-based Hardware/Software EEG system (Synamps 2, Scan 4.3 Acquire, Neuroscan; Compumedics) with four Ag-AgCl scalp electrodes, differentially recorded from the center vertex of the head (Cz, active) to linked earlobe references, with the forehead used as ground. Contact impedance was < 5k Ω for all electrodes. Filtering, epoching, artifact rejection, and averaging were performed offline using Scan 4.3 (Neuroscan; Compumedics). For each musical interval, ~6,000 trials were collected (3,000 per stimulus polarity). Responses were bandpass filtered from 20 to 2,000Hz (12 dB/oct roll off), and trials with activity outside the range of $\pm 35\mu\text{V}$ were considered artifacts and rejected, such that the final number of trials per condition was 6000 ± 100 . Responses of alternating polarities were added together to isolate the neural response by minimizing the stimulus artifact and cochlear microphonic (Gorga, Abbas, & Worthington, 1985; Skoe & Kraus, 2010a). The process of adding also

TABLE 3. Amplitude of Each Stimulus Frequency Component Relative to the Amplitude of the f0 of the Upper Tone, E3 for the Consonant (Top) and Dissonant (Bottom) Intervals

Perfect 5 th				Major 6 th			
Upper E3	Amplitude ratio	Lower A2	Amplitude ratio	Upper E3	Amplitude ratio	Lower G2	Amplitude ratio
F0	1	F0	0.93	F0	1	F0	0.74
H2	0.30	H2	0.53	H2	0.21	H2	0.43
H3	0.07	H3	0.30	H3	0.07	H3	0.23
H4	0.01	H4	0.07	H4	0.01	H4	0.05
		H5	0.02			H5	0.07
		H6	0.01				
minor 7 th				minor 2 nd			
Upper E3	Amplitude ratio	Lower F#2	Amplitude ratio	Upper E3	Amplitude ratio	Lower D#3	Amplitude ratio
F0	1	F0	0.76	F0	1	F0	1.32
H2	0.21	H2	0.44	H2	0.23	H2	0.21
H3	0.07	H3	0.23	H3	0.07	H3	0.13
H4	0.01	H4	0.05	H4	0.01	H4	0.01
		H5	0.02				

accentuates the lower-frequency components of the response including phase locking to the amplitude envelope of the stimulus (Goblick & Pfeiffer, 1969; Skoe & Kraus, 2010a).

ANALYSIS

Periodicity. Autocorrelation analysis was used to evaluate the periodicity of the stimuli and responses. The resulting autocorrelations (lag vs. correlation coefficient r) graphically represent signal periodicity over the course of a waveform. Autocorrelation was performed on 150 ms bins of the response starting at 50 ms. The maximum (peak) autocorrelation value (expressed as a value between -1 and 1) was recorded for each bin, with higher values indicating more periodic timeframes (150 total bins, 1 ms interval between the start of each successive bin). The strength of the periodicity was calculated as the average of the autocorrelation peaks (maximum r values) across the 150 bins for each subject.

Distortion products. To evaluate the frequency composition of the response, Fourier analysis was performed over the frequency-following response (FFR) (Moushegian, Rupert, & Stillman, 1973), the most periodic portion of the response (50-350 ms). The onset response was not included in this window of analysis given that the onset does not convey pitch-related information of interest. The visual display of the computed spectra (Figure 5) has a resolution of 1 Hz; smoothing of the spectrum was achieved by zero padding the FFR to 1s prior to performing the fast Fourier transform (FFT). The spectra were analyzed only up to 700 Hz because

a majority of the spectral components above 700 Hz fell below the noise floor. To estimate the spectral noise floor, an FFT was performed on a 50 ms time window prior to the stimulus onset (-50 to 0 ms). The spectral noise floor estimates were used to calculate spectral signal to noise ratios (SNRs) of the individual peaks in the spectrum of the FFR.

In each response spectrum, we identified peaks of interest based on the frequency components of each stimulus and the putative DPs resulting from the interaction of the frequency components. For putative DPs, we considered only additions and subtractions of the frequencies of two primary notes (f_1 and f_2), their harmonics (no higher than the fourth harmonic), the common subharmonics of f_1 and f_2 , and the harmonics of the common subharmonics. For each peak of interest, we tallied the number of subjects for which the peak was reliably present in the response spectrum. To be counted in this tally, the following criteria needed to be met: (1) the peak must have an SNR of more than 1.5. (2) When the SNR is less than 3, the peak must be larger in amplitude or equivalent in amplitude to the two neighboring peaks. (3) The frequency of the peak must be within ± 3 Hz range of the target frequency, with the target frequency corresponding to either of the f_0 s, their harmonics, or putative DPs of the intervals. However, if the width of the peak encompassed the target frequency but the peak itself deviated from the ± 3 Hz range, the peak was counted if the SNR at the target frequency exceeded 1.5. If the target frequency was not a local maximum, it was dismissed and not counted in the tally (See Supplementary Table 1 for a list of the significant peaks for

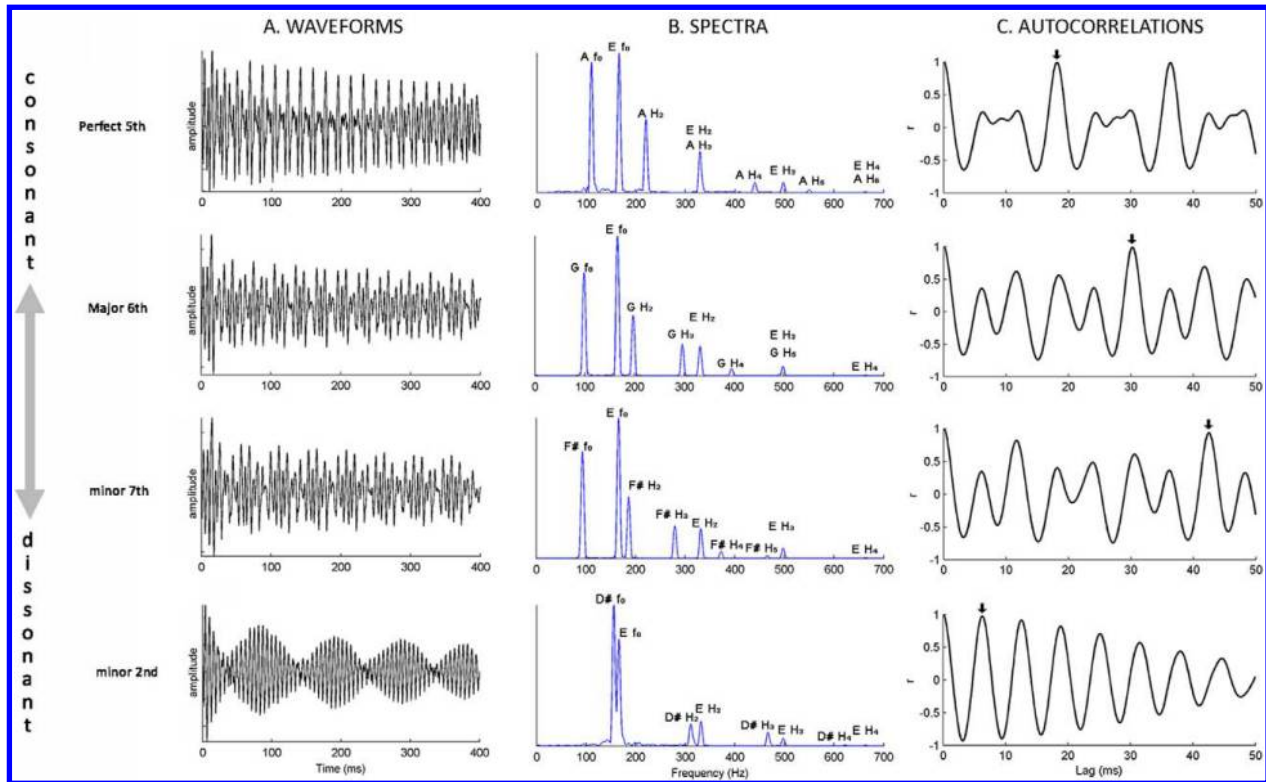


FIGURE 1. Four musical intervals ranging in their levels of consonance: Perfect 5th, Major 6th, minor 7th, and minor 2nd (from top to bottom, respectively). P5 is the most consonant among these four intervals, followed by M6 and m7, with m2 being the most dissonant. The temporal and spectral characteristics of the waveforms are graphically represented in this figure. The time-amplitude waveforms of the stimuli are plotted in panel A, the frequency spectra of the waveforms are plotted in panel B, and panel C includes the stimulus autocorrelations. For the autocorrelations, the time indicated on the x-axis refers to the lag of the autocorrelation function. Y-axis indicates the degree of periodicity, and the arrows indicate the highest periodicity for each stimulus.

each of the four intervals along with the respective target frequencies. Included in the table is the percentage of subjects in whom the peak is reliably detected).

In Figure 1, the four stimuli are graphed to illustrate their temporal and spectral characteristics. For the stimulus autocorrelations, the periodicity displayed on the upper limit of the y-axis (50 ms) corresponds to 20 Hz, the lowest frequency limit of the human periodicity pitch percept (Moore, 1997). The strong harmonic relationship between stimulus spectral components in a consonant interval produces highly periodic stimulus waveforms. The dominant periodicity of the two consonant intervals corresponds to the common subharmonic (Cariani, 2001, 2004; Tramo et al., 2001) of the two notes of the interval (18.15 ms, 55 Hz for P5 and 30.25 ms, 33 Hz for M6). For the two dissonant intervals, the common subharmonic is 18.5 Hz for m7 and 10.4 Hz for m2, but the highest periodicity falls at 42.45 ms (23.56 Hz) for m7 and 6.25 ms (160.00 Hz) for m2. The strength of highest periodicity

(r) was .9955 for P5, .9899 for M6, .9255 for m7, and .9708 for m2.

Results

PERIODICITY: AUTOCORRELATION ANALYSIS

Figure 2 displays the autocorrelations of the responses to the four musical intervals. The highest response periodicity was at 18.15 ms (the period of 55 Hz) for P5, 30.30 ms (33 Hz) for M6, 42.40 ms (23.58 Hz) for m7, and 18.60 ms (53.76 Hz) for m2. Figure 3 graphically depicts the average strength of the highest periodicity in the ABR across the group of participants. Results of the repeated-measures ANOVA showed a significant effect of musical interval on the strength (r) of the highest periodicity, $F(3, 76) = 210.10$, $p < .0001$. Post hoc Tukey tests were used to evaluate all pair wise multiple comparisons, and all comparisons showed significant differences (all $p < .01$). That is, the more dissonant the interval, the less periodic the response. Specifically, the

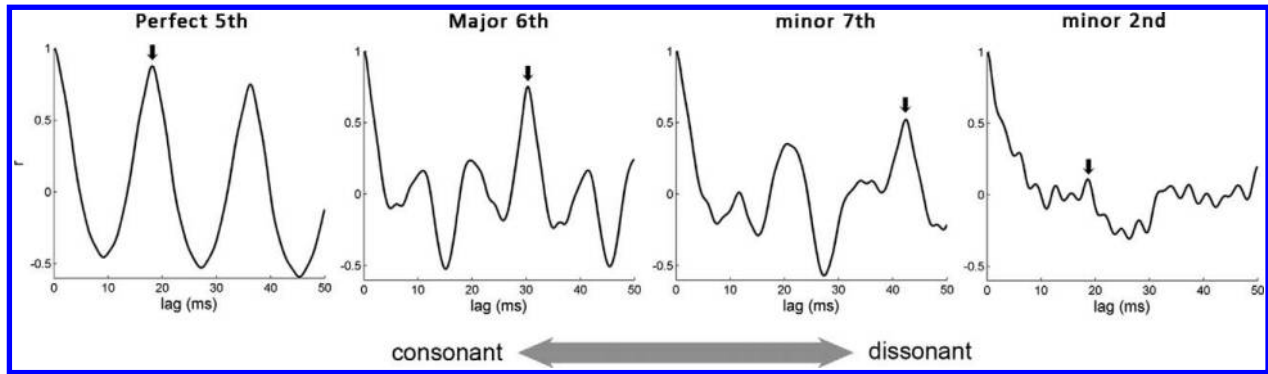


FIGURE 2. The autocorrelation of the response to each musical interval. The time indicated on the x-axis refers to the lag of the autocorrelation function. Y-axis indicates the degree of periodicity. Arrows indicate the cycle of the highest periodicity. This figure was generated using the grand average time-domain response waveform for each interval.

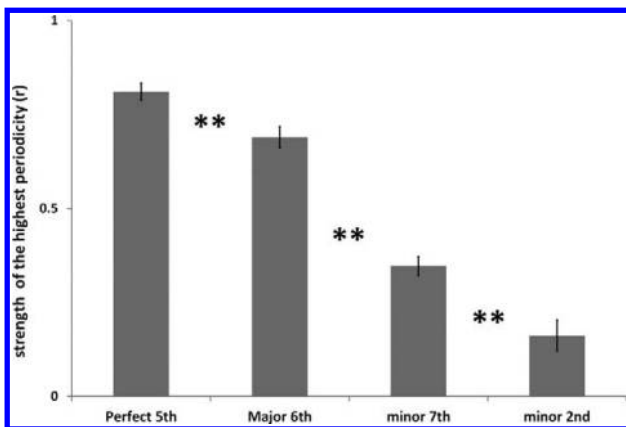


FIGURE 3. The strength (r) of the highest periodicity of the response to each musical interval averaged across participants. The more consonant interval, the more periodic the response. For consonant intervals, P5 and M6, the highest periodicity occurred at the period corresponding to the common subharmonic. Errorbars indicate one standard error of the mean; $**p < .01$

strength of the highest periodicity was significantly larger for P5 ($r = .81$) than for the other three intervals, $p < .01$. M6 was significantly larger than m7 ($r = .69$ for M6 and $r = .35$ for m7, $p < .001$), and m7 was significantly larger than m2 ($r = .16$ for m2, $p < .001$).

The highest periodicity of the stimulus and response matched (i.e., were identical) for all intervals but m2. Specifically, in both the stimulus and the response, the highest periodicity occurred at 18.15 ms for P5, 30.30 ms for M6, and 42.40 ms for m7. For P5 and M6, the highest periodicity corresponds to the period of the common subharmonic. However, for the most dissonant interval, m2, the highest periodicity of the response (18.60 ms, the period of 53.76 Hz) was different from that of the stimulus (6.25 ms, 160.00 Hz) and it decayed rapidly

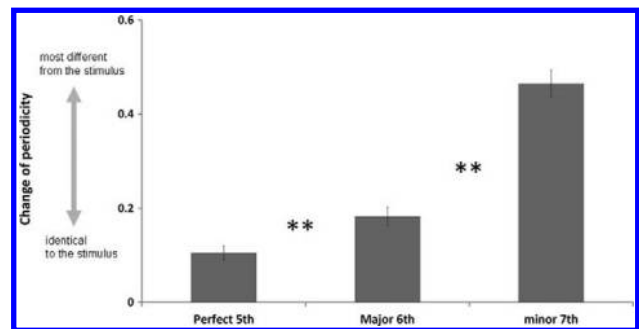


FIGURE 4. The extent to which the response periodicity (at the common subharmonic) deviates from the stimulus periodicity. The more dissonant an interval, the bigger the discrepancy in the periodicity strength (r) from the stimulus to the response. That is, whereas the periodicity of the most consonant interval (P5) was faithfully represented in the brainstem response, that of the dissonant interval (m7) was weakened. Errorbars indicate one standard error of the mean; $**p < .01$.

with increasing multiples of the period, as indicated by a decrease in periodicity at 37.50 ms. To examine how faithfully the highest periodicity of the stimulus was reflected in the ABR, we calculated the change in the strength (r) between the stimulus ($r_{stimulus}$) and the response ($r_{response}$) using this formula: $(r_{stimulus} - r_{response}) / (r_{stimulus} + r_{response})$ (Figure 4). This dependent variable was calculated only for three intervals, P5, M6, and m7, for which there was a match between the highest periodicity of the stimulus and response. Using this metric, we found a significant effect of musical interval on the faithfulness with which the stimulus periodicity was preserved in the response, $F(2, 27) = 77.43$, $p < .001$. Moreover, all pairwise comparisons showed significant differences, as indicated by post hoc Tukey tests. The change in response periodicity was

smaller for P5 than for M6, $p < .05$, and m7, $p < .001$, while M6 showed a smaller change than m7, $p < .001$. Thus, this result indicates that the more dissonant an interval, the less faithfully the periodicity of the stimulus was represented in the response.

DISTORTION PRODUCTIONS: SPECTRA OF FOUR INTERVALS

To investigate how the subcortical transformation of periodicity is related to DPs, we evaluate the frequency composition of the response by using Fourier analysis. In addition to the f_0 s and harmonics of two tones, the response spectra contained peaks corresponding to frequencies that do not physically exist in the stimulus spectra. Most of these additional peaks represented DP frequencies arising from the nonlinear manner in which the auditory system processes the acoustic interaction between single tones (and their harmonics) comprising the interval. Our previous study provided evidence that these peaks are not acoustic or electric artifacts arising from the presentation or collection hardware or software. When we presented the original stimuli (M6 and m7) through the Neuroscan and Ety-motic equipment into a Bruel & Kjaer 2-CC coupler and recorded the output, the output waveform did not include any spectral components corresponding to DPs observed in the ABR (for details see Lee et al., 2009).

Figure 5 displays the average ABR spectra for each of the four musical intervals. The more dissonant the interval, the more additional response peaks were found. Whereas the consonant intervals, P5 and M6, contained on average only 4 and 12 additional peaks (respectively), the dissonant intervals, m2 and m7, contained 28 and 19 additional peaks (respectively) between 0 and 700 Hz.

In addition to containing more spectral peaks than the more consonant conditions, for the minor second, the peaks were less separated and regularly spaced in frequency. Specifically, in the average response spectrum of the most consonant interval, P5, the average distance between consecutive peaks was 54.90 Hz ($SD = 1.27$ Hz). For M6, the second-most consonant interval, the average distance between peaks (33.05 Hz) was smaller than P5, t test, $p < .001$, but larger than m7 (24.73 Hz, t test, $p < .01$). In the case of m2, the most dissonant interval, the spectrum contained the smallest average interval between peaks (18 Hz). Only for the two consonant intervals, P5 and M6, does the average distance equal the frequency of the common subharmonic of two tones. This indicates that all multiple frequencies of the common subharmonic were represented in the response spectrum. The standard deviation was 1.27 Hz for P5,

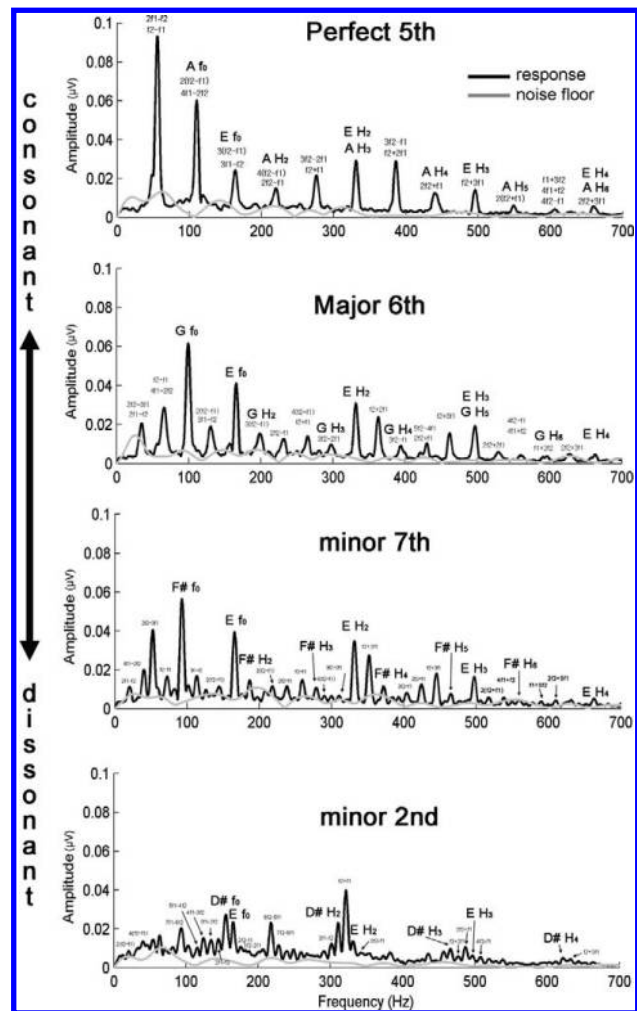


FIGURE 5. Response spectra for the four musical intervals used in this study. Each response spectrum represents the average of ten subjects. Peaks labeled in the small font denote DPs, i.e., frequency components that do not exist in stimuli. f_1 denotes the lower tone and f_2 denotes the upper tone of each interval. The gray line indicates the spectral noise floor.

1.81 Hz for M6, 11.74 Hz for m7, and 20.48 Hz for m2. Thus, the spectrum of m2 showed what could be considered the lowest level of regularity between response components among the four intervals.

Discussion

By investigating the auditory brainstem responses to four musical intervals with varying degrees of consonance, this study sought to examine how auditory nonlinearities transform the acoustic characteristics of the musical intervals, and how this transformation might depend on the degree of consonance. Our analysis revealed that

the more dissonant the interval, the less periodic the responses, and the greater the discrepancy between the periodicity of the stimuli and response.

THE REDUCED PERIODICITY OF DISSONANT INTERVALS BY AUDITORY SYSTEM NONLINEARITIES

Periodicity is an important acoustic factor for discriminating consonant and dissonant intervals. The more dissonant an interval, the less periodic the signal is; in fact, Stolzenburg (2013) demonstrated that the degree of consonance could be precisely predicted by the periodicity that is mathematically derived from the frequency ratio of the tones comprising a musical interval. It is well known that the periodicity of an auditory stimulus is encoded by neural phase locking from the peripheral to the central stage of the auditory system. Our study provides physiological evidence that the periodicity of musical interval is represented in the human brainstem. More periodic brainstem responses to consonant intervals are consistent with previous neuronal recordings in the auditory nerve, midbrain, and cortex of animals that showed more precise neural synchrony for consonant intervals over dissonant intervals (Fishman et al., 2001; McKinney et al., 2001; Tramo et al., 2001). Our result is also in line with mathematical models explaining sensory consonance with a neuronal periodicity detection mechanism (Ebeling, 2008; Langner, 1997, 2005).

While the periodicity of the consonant interval is well preserved in the brainstem response, that of the dissonant interval is less accurately represented, as seen by a large discrepancy between the periodicity of the stimulus and response. Specifically, the weak periodicity of the dissonant stimulus was further weakened in the brainstem response. It seems that the nonlinear properties of the brainstem reduce the periodicity of dissonant intervals and thereby enhance the periodicity differences between consonant and dissonant intervals. Given the superior phase locking of the auditory system to periodic signals, the efficiency of neural encoding may possibly decrease when processing signals that are aperiodic, including the dissonant intervals used in this study.

How does the neural transformation of dissonant interval influence the perception of sensory dissonance and consonance? A recent study (Bones et al., 2014) found that diotic presentation of consonant intervals, compared to dichotic presentation, increases the perception of consonance. In contrast, the dissonant interval included in the Bones et al. study, m2, was rated less pleasant in the diotic condition. That is, when two tones of the dissonant interval were presented to the

same ear, the interval was judged more unpleasant. For consonant intervals, they demonstrated that increased interactions of two tones for diotic presentation result in additional DPs and these DPs enhance the harmonicity of consonant intervals. However, there was no explanation as to why dissonant intervals presented in the diotic condition were judged more dissonant. Our result suggests that increased interactions of two tones in the diotic condition facilitate nonlinear neural transformations, and that this transformation in turn contributes to the increased perception of dissonance. One interpretation of our findings is that the auditory system alters the dissonant intervals in such a way that they become more dissonant than would be the case if they were processed by a linear auditory system.

However, given that FFR is a population response and it registers only synchronized portions of the neural population response, it is also possible that the periodicity of dissonant intervals is faithfully represented by individual neurons but that these activities, by virtue of their small number and/or the phase of their firing, are not reflected in the FFR.

ADDITIONAL DISTORTION PRODUCTS OF THE DISSONANT INTERVAL

The spectral analysis revealed that dissonant intervals have a larger number of additional DPs that are not present in the stimulus spectrum. Those additional DPs are close in frequency to the original harmonic components of the intervals, whereas DPs generated by consonant intervals are widely spaced or coincided with the harmonic components of the stimulus.

Helmholtz hypothesized that the perception of dissonance results from the roughness that arises from the interaction of partials (a general term for spectral components composing a complex sound) that are close in frequency (Helmholtz, 1877/1954). Behavioral studies have shown that sounds with widely spaced partials such as clarinet tones, which include only odd harmonics, are more consonant sounding than sounds with narrowly spaced partials (Rasch & Plomp, 1982). In addition, experiments using sounds with inharmonic partials (Pierce, 1966; Slaymaker, 1970) have shown that consonance and dissonance ratings are indeed dependent on the coincidence of partials. Thus, it is possible that the narrowly spaced DPs and harmonic components of dissonant intervals increase roughness by creating additional spectral interferences, and make the intervals more dissonant.

It remains to be examined whether the DPs do indeed interact with the original spectral components or other DPs to influence the perception of consonance or

dissonance. Historically, Helmholtz (1877/1954) and Krueger (1913) suggested that perceptual beating between difference tones of a musical interval may contribute to dissonance. Indeed, single neuron responses to a mistuned complex tone in the chinchilla IC (Sinex, Henderson Sabes, & Li, 2002) show fluctuations reflecting second-order interactions between two response components corresponding to first-order frequency differences, as well as fluctuations corresponding to simple differences between the frequencies of stimulus components, suggesting that interactions between DPs are evident in the neural response.

NEURAL EVIDENCE OF THE COMMON SUBHARMONIC (FUNDAMENTAL BASS)

The spectral analysis shows that a common subharmonic is represented as a distortion product (DP) in the auditory brainstem response and the highest periodicity of response also occurs at a period corresponding to the common subharmonic for consonant intervals. However, for dissonant intervals, a common subharmonic is not significantly present (for m2) or else it shows relatively weak periodicity (for m7) in the responses. The common subharmonic is what Rameau theoretically suggested to be the *basse-fondamentale* (fundamental bass) in his *Treatise on Harmony* (1722/1971). Terhardt (1984) postulated that this bass note of a musical chord is identical in nature to the virtual pitch of individual complex tones and that consonance is determined by the degree to which the spectral components of a musical interval evoke a strong and unified sensation of this fundamental bass. Tramo et al. (2001) found that the bass note was reflected in cat auditory nerve responses to consonant intervals. Likewise, our study shows that the human brainstem response to musical intervals represents the fundamental bass. Such a finding is also consistent with previous human work using sine waves and sounds composed of single harmonic tones, which have shown that virtual pitches are represented in the temporal discharge patterns of neurons in the rostral brainstem (Chertoff & Hecox, 1990; Chertoff, Hecox, & Goldstein, 1992; Elsisy & Krishnan, 2008; Galbraith & Doan, 1995; Greenberg, Marsh, Brown, & Smith, 1987; Pandya & Krishnan, 2004; Rickman, Chertoff, & Hecox, 1991; Skoe and Kraus, 2010b). However, because our previous study revealed that DPs are more robust in musicians relative to nonmusicians (Lee et al., 2009), it is possible that our current findings apply only to musicians, as with the group measured here, and different mechanisms may be at work in individuals with less or no music training.

THE ORIGINS OF DISTORTION PRODUCTS

Our methodology does not allow us to pinpoint the specific origins of the DPs. The DPs found in the brainstem responses to musical intervals could reflect the cochlear DPs and/or neural DPs generated by the nonlinearities of the central auditory system. Moreover, the common subharmonic of two tones that arise in the neural response are possibly attributed to different DP sources, and the source may even depend on the specific musical interval. For example, the common subharmonic of P5, 55 Hz, corresponds to a $2f_1-f_2$ and f_2-f_1 relationship, whereas the 33 Hz subharmonic of M6 corresponds to $2f_1-f_2$ and $2f_2-3f_1$. $2f_1-f_2$ and $2f_2-3f_1$ are DPs that are commonly measured in distortion product otoacoustic emissions (DPOAEs), sounds that can be measured using small microphones placed inside the ear canal. DPOAEs result from the nonlinearity of outer hair cell motion (Rhode & Cooper, 1993; Robles, Ruggero, & Rich, 1991). However, the $2f_1-f_2$ DP produced by a wide frequency ratio, such as 1.67 (166 Hz/99 Hz) of M6, has been very rarely demonstrated in the DPOAE (Dhar, Long, Talmadge, & Tubis, 2005; Knight & Kemp, 1999, 2000, 2001) and the amplitude of the cochlear DPs rapidly decreases as the frequency ratio between the two simulating tones increases (Goldstein, 1967). Thus, it is possible that the $2f_1-f_2$ DP of M6 is not a cochlear DP, but a neural DP. Regarding f_2-f_1 , direct measurements of the chinchilla IC responses to mistuned tones (Sinex et al., 2002), double complex tones (Sinex & Li, 2007), the guinea pig cochlear nerve responses to double vowels (Palmer, 1990) as well as the human ABRs to complex tones (Wile & Balaban, 2007) have provided evidence that f_2-f_1 reflects envelope-related neural activity.

Some of the DPs measured in the brainstem response may possibly reflect second-order interactions between components — for example, interactions between two DPs corresponding to the first-order interaction or between a DP and spectral component that is physically present in the stimulus spectrum. Sinex and colleagues have shown that single neuron responses to mistuned complex tone in the chinchilla IC (Sinex & Li, 2007) exhibit fluctuations that reflect second-order interactions between two response components corresponding to first-order frequency differences. Moreover, recent studies on amplitude modulation have demonstrated that second-order amplitude modulation, which occurs when the amplitude modulation varies sinusoidally as a function of time, produces additional sidebands around the first-order frequency components in the modulation spectrum of the stimulus (Lorenzi, Simpson, et al., 2001; Lorenzi, Soares, & Vonner, 2001; Millman, Green,

Lorenzi, & Rees, 2003). It has been suggested that some nonlinear mechanism along the auditory pathway must generate an audible distortion component at the envelope beat rate in the “internal” modulation spectrum of complex temporal envelopes (Füllgrabe, Meyer, & Lorenzi, 2003; Lorenzi, Soares, & Vonner, 2001). In addition, Füllgrabe et al. (2003) compared first- and second-order amplitude modulation detection thresholds of normal hearing and hearing impaired listeners and found that cochlear damage has no effect on the detection of complex temporal envelopes. This result indicates that a subset of distortion components are likely generated by a more central nonlinearity.

It is also possible that DPs found in our study reflect the interactions at the level of the cochlea, auditory nerve, cochlear nucleus, dorsal nucleus of the lateral lemniscus (DNLL), and/or inferior colliculus, because previous work using musical intervals (Bidelman & Krishnan, 2009) did not find DPs in the brainstem response spectrum when the two notes were presented to separate ears (dichotic presentation). The use of diotic stimulation (both sounds to both ears) in the present study likely contributed to stronger amplitude modulation (or beats) that resulted from the interaction of adjacent spectral components. This interaction could take place in peripheral and/or central stages of the auditory system, but given that DPs were reported to be absent from brainstem response when two tones are presented dichotically (Bidelman & Krishnan, 2009), DPs may reflect interactions that occur peripheral to the superior olivary nucleus, one of the earliest major sites of binaural interaction. Further investigation on

how DPs change with more strictly controlled stimuli should provide us greater insight into the nonlinearities of the auditory system.

Conclusion

The periodicity of a musical interval has been known for many years to be an important factor for determining the degree of consonance and dissonance (Ebeling, 2008; Gill & Purves, 2009; Langner, 1997, 2005; Stolzenburg, 2013). Our results demonstrate that, due to the nonlinear nature of the auditory system, the neural representation of dissonant musical intervals is made more discrete from that of consonant intervals with an intensified aperiodicity in the subcortical level of the auditory system.

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Supplementary Tables

TABLE 1-1. Response Frequencies in the Auditory Brainstem Response to P5, the Most Consonant Interval

Perfect 5 th			
Expected frequency (Hz)	Frequency relationship	Response frequency (Hz)	% of Subjects
54	2f1-f2	56	100%
55	SH		
56	f2-f1		
108	4f1-2f2	110	100%
110	f1, 2SH		
112	2(f2-f1)		
164	3f1-f2	163	100%
165	3SH		
166	f2		
168	3(f2-f1)		
220	2f1, 4SH	220	100%
222	2f2-f1		
224	4(f2-f1)		
275	5SH	276	100%
276	f2+f1		
278	3f2-2f1		
330	3f1,6SH	331	100%
332	2f2		
385	7SH	386	100%
386	f2+2f1		
388	3f2-f1		
440	4f1, 8SH	440	90%
442	2f2+f1		
495	9SH	496	100%
496	f2+3f1		
498	3f2		
550	5f1, 10SH	549	100%
552	2f2+2f1		
605	11SH, 4f2-f1	606	90%
606	4f1+f2		
608	f1+3f2		
660	12SH, 6f1	660	100%
662	2f2+3f1		
664	4f2		

Note: Frequencies of f_0 s, harmonics, and DPs present in the auditory brainstem responses to four musical intervals. f_1 denotes the lower tones and f_2 denotes the upper tone of each interval. The values in the expected frequency column were calculated based on the frequency of the f_0 s and harmonics of stimuli as well as the putative DPs resulting from the interaction of the spectral components. For putative DPs, we considered only additions and subtractions of the frequencies of two primary notes (f_1 and f_2), their harmonics (no higher than the fourth harmonic), the common subharmonics (SH) of f_1 and f_2 , and its harmonics (2SH = second harmonic of SH, 3SH = third harmonic of SH, etc.). Response frequency refers to the frequency at which that the response peak occurred. Percentage of subjects indicates the degree to which the peak is reliably present within the subject pool. NS (not significant) indicates spectral components that were predicted but were not reliably present in the average response spectra.

TABLE 1-2. Response Frequencies in the Auditory Brainstem Response to M6, the Second Most Consonant Interval

Major 6 th			
Expected frequency (Hz)	Frequency relationship	Response frequency (Hz)	% of subjects
32	2f1-f2	35	100%
33	SH		
35	2f2-3f1		
64	4f1-2f2	66	100%
66	2SH		
67	f2-f1		
99	f1, 3SH	99	100%
131	3f1-f2	130	90%
132	4SH		
134	2(f2-f1)		
165	5SH	166	100%
166	f2		
198	2f1, 6SH	199	80%
201	3(f2-f1)		
231	7SH	232	100%
233	2f2-f1		
264	8SH	265	90%
265	f2+f1		
268	4(f2-f1)		
297	3f1, 9SH	297	90%
300	3f2-2f1		
330	10SH	332	100%
332	2f2		
363	11SH	363	100%
364	f2+2f1		
396	4f1, 12SH	396	80%
399	3f2-f1		
429	13SH	430	100%
431	2f2+f1		
462	14SH	462	90%
463	f2+3f1		
495	5f1, 15SH	498	100%
498	3f2		
528	16SH	529	90%
530	2f2+2f1		
561	17SH	560	80%
562	4f1+f2		
565	4f2-f1		
594	6f1, 18SH	596	60%
597	f1+3f2		
628	19SH	628	100%
629	2f2+3f1		
660	20SH	663	100%
664	4f2		

TABLE 1-3. Response Frequencies in the Auditory Brainstem Response to m7, the Second Most Dissonant Interval.

minor 7 th			
Expected frequency (Hz)	Frequency relationship	Response frequency (Hz)	% of subjects
18.5	SH	20	80%
20	2f1-f2		
37	2SH	40	100%
40	4f1-2f2		
53	2f2-3f1	52	100%
55.5	3SH		
73	f2-f1	72	90%
74	4SH		
92.5	5SH	93	100%
93	f1		
111	6SH	113	100%
113	3f1-f2		
129.5	7SH	NS	
146	2(f2-f1)	145	100%
148	8SH		
166	f2	166	100%
166.5	9SH		
185	10SH	186	90%
186	2f1		
203.5	11SH	NS	
219	3(f2-f1)	218	100%
222	12SH		
239	2f2-f1	238	80%
240.5	13SH		
259	f2+f1, 14SH	259	90%
277.5	15SH	279	100%
279	3f1		
296	16SH	NS	
314.5	17SH	NS	
332	2f2	332	100%
333	18SH		
351.5	19SH	352	100%
352	f2+2f1		

(continued)

Table 1-3. (continued)

minor 7 th			
Expected frequency (Hz)	Frequency relationship	Response frequency (Hz)	% of subjects
370	20SH	372	100%
372	4f1		
388.5	21SH	NS	
405	3f2-f1	404	80%
407	22SH		
425	2f2+f1	424	90%
425.5	23SH		
444	24SH	445	100%
445	f2+3f1		
462.5	25SH	465	100%
465	5f1		
481	26SH	NS	
498	3f2	497	90%
499.5	27SH		
		506*	80%
518	2f2+2f1,28SH	517	90%
536.5	29SH	538	90%
538	4f1+f2		
555	30SH	559	60%
558	6f1		
573.5	31SH	NS	
591	f1+3f2	590	70%
592	32SH		
610.5	33SH	610	80%
611	2f2+3f1		
629	34SH	NS	
647.5	35SH	NS	
664	4f2	663	90%
666	36SH		
684.5	37SH	NS	

Note: * indicates the frequency that is not predicted from the spectral composition of the stimulus, but is present in the response spectrum.

TABLE 1-4. Response Frequencies in the Auditory Brainstem Response to m2, the Most Dissonant Interval

minor 2 nd			
Expected frequency (Hz)	Frequency relationship	Response frequency (Hz)	% of subjects
10.4	SH	NS	
20	2(f2-f1)	20	90%
20.8	2SH		
31.2	3SH	NS	
40	4(f2-f1)	40	80%
41.6	4SH		
52	5SH	NS	
62.4	6SH	63	100%
72.8	7SH	71	40%
83.2	8SH	82	70%
93.6	9SH	93	100%
104	10SH	NS	
114.4	11SH	116	90%
124.8	12SH	124	100%
126	4f1-3f2		
135.2	13SH	135	100%
136	3f1-2f2		
145.6	14SH	145	90%
146	2f1-f2		
156	f1, 15SH	155	100%
166	f2	165	100%
166.4	16SH		
176	2f2-f1	176	100%
176.8	17SH		
186	3f2-2f1	182	50%
187.2	18SH		
197.6	19SH	200	60%
208	20SH	NS	
218.4	21SH	218	100%
228.8	22SH	228	70%
239.2	23SH	NS	
249.6	24SH	249	100%
260	25SH	259	70%
270.4	26SH	NS	
280.8	27SH	NS	
291.2	28SH	NS	
301.6	29SH	302	70%
302	3f1-f2		
312	2f1, 30SH	311	100%
322	f2+f1	321	100%
322.4	31SH		
332	2f2	331	100%
332.8	32SH		

(continued)

Table 1-4. (continued)

minor 2 nd			
Expected frequency (Hz)	Frequency relationship	Response frequency (Hz)	% of subjects
342	3f2-f1	342	80%
343.2	33SH		
353.6	34SH	354	70%
364	35SH	NS	
374.4	36SH	NS	
384.8	37SH	NS	
395.2	38SH	NS	
405.6	39SH	NS	
416	40SH	NS	
426.4	41SH	NS	
436.8	42SH	NS	
447.2	43SH	NS	
457.6	44SH	457	90%
468	3f1, 45SH	466	90%
478	f2+2f1	477	90%
478.4	46SH		
488	2f2+f1	487	100%
488.8	47SH		
498	3f2	497	100%
499.2	48SH		
508	4f2-f1	508	90%
509.6	49SH		
520	50SH	519	80%
530.4	51SH	NS	
540.8	52SH	538	90%
551.2	53SH	NS	
561.6	54SH	NS	
572	55SH	NS	
582.4	56SH	NS	
592.8	57SH	NS	
603.2	58SH	NS	
613.6	59SH	NS	
624	4f1, 60SH	622	90%
634	f2+3f1	632	80%
634.4	61SH		
644.8	62SH	NS	
655.2	63SH	NS	
664	4f2	NS	
665.6	64SH	NS	
676	65SH	NS	
686.4	66SH	NS	
696.8	67SH	NS	