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Olivier Macherey. Sensitivity to temporal fine structure probed with pulse-spreading harmonic complexes. International Symposium on hearing, Jun 2022, Lyon, France. hal-03876570

HAL Id: hal-03876570

<https://cnrs.hal.science/hal-03876570>

Submitted on 28 Nov 2022

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Sensitivity to temporal fine structure probed with pulse-spreading harmonic complexes

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Abstract

Temporal fine structure (TFS) is assumed to play an important role in both pitch and speech processing in normal hearing (NH). However, there is still some debate on how TFS is coded in the auditory periphery. Moore & Sek (2009) provided evidence that NH subjects are sensitive to TFS at very high frequencies in stimulus conditions where spectral cues should not be present. This is important because it implies that phase locking may still provide useful information above 4000 Hz where it is commonly believed to be absent. Here, we examine sensitivity to TFS using different stimuli than the frequency-shifted complexes previously used. Pulse-spreading harmonic complexes (PSHCs) are spectrally-dense complexes with a low f_0 (here 2 Hz). The phase of the components is set so that the envelope rate can be manipulated independently from the f_0 . Here, we use a special case of PSHCs for which the TFS peaks were shifted relative to the envelope peaks from one envelope period to the next. For upward PSHCs (up-PSHC), the TFS peaks were progressively advanced, yielding a rising pitch percept across the stimulus, while for downward PSHCs (down-PSHC), the peaks were progressively delayed, yielding a falling pitch percept. In Experiment 1, subjects heard up-PSHC, down-PSHC and regular inharmonic complexes bandpass-filtered with a lower cut-off (F_c) of 2000 Hz and were asked to identify whether the pitch was rising, falling or flat in a one interval, three alternative forced choice task. The envelope rate was 98, 200 or 450 pps. For the two highest rates, most subjects correctly identified the direction of the pitch change while for the lowest rate, the stimuli could not be discriminated. This shows that, for a given F_c , there is an envelope rate below which the auditory system is insensitive to changes in TFS. The lower rate limit of TFS sensitivity was measured in Experiment 2 using an adaptive three interval, two alternative forced choice task where subjects heard two down-PSHC and one up-PSHC and had to pick the latter. The stimuli were bandpass filtered in seven frequency regions with F_c varying from 250 to 11200 Hz and were presented in the presence of threshold-equalising noise. The lower limit significantly increased from 42 pps to 691 pps with increases in F_c . The ratio between F_c and the envelope rate at threshold also increased from 6 to 18 when F_c increased from 250 to 2000 Hz, then remained flat with further increases in F_c or slightly decreased at the highest F_c . In the lower part of the spectrum (<2000 Hz), this lower limit resembles the lower limit of melodic pitch. The results in the upper part of the spectrum suggest that TFS cues are still available in high frequency regions (up to 10 kHz) when the rank of the lowest harmonic present in the passband is 18, and all harmonics are presumably unresolved.

39 Introduction

40 The spectral decomposition performed by the cochlea resembles that achieved by a bank of
41 overlapping bandpass filters: in response to a sound, the vibration pattern of a particular point
42 on the basilar membrane corresponds to a bandpass-filtered version of the original sound
43 waveform. This filtered waveform can be decomposed into a slowly varying envelope
44 superimposed on a carrier, referred to as the temporal fine structure (TFS), which oscillates at a
45 rate close to the characteristic frequency of this particular cochlear location. Auditory nerve
46 fibers can, to some extent, phase-lock to this TFS and there is evidence that this temporal neural
47 information is used by the binaural system for frequencies up to about 1400 Hz (Zwislocki &
48 Feldman, 1956). The exact limit of phase locking in humans and whether or not it is important for
49 pitch perception remain, however, a matter of debate. Most animal species exhibit a steep
50 decrease in phase locking for frequencies above about 1000 or 2000 Hz (Koppl, 1997). The
51 finding that pure tone frequency discrimination in humans also deteriorates for frequencies
52 above 2000 Hz has often been cited as evidence that frequency discrimination depends on phase
53 locking information (e.g., Moore & Ernst, 2012). However, Oxenham et al. (2011) reported that
54 harmonic complex tones only containing components above 4000 Hz can still convey a clear,
55 musical pitch percept. They concluded either that phase locking information is not needed for
56 complex pitch perception or that it is still usable by humans at these very high frequencies.

57 Moore & Sek (2009) investigated sensitivity to TFS at very high frequencies (above 8 kHz) by
58 asking their subjects to discriminate between bandpass filtered harmonic and inharmonic
59 complex tones. In each trial, the inharmonic complex contained the same components as the
60 harmonic complex except the components were shifted by a fixed amount in Hz. These two
61 stimulus waveforms have identical envelopes but different TFS. Moore & Sek (2009) showed that
62 subjects could discriminate between these two stimuli when the lowest harmonic present in the
63 passband was the 12th. According to usual definitions of resolvability (Moore & Gockel, 2011),
64 this would imply that the components were unresolved and that the subjects could not use
65 differences in excitation patterns to perform the task. They, therefore, concluded that TFS
66 sensitivity was mediated by phase locking information which in turn implied that phase locking
67 cues could still be used by their subjects at frequencies higher than 8 kHz. This is controversial
68 because as previously mentioned, animal experiments show poor phase locking at these
69 frequencies and there are currently no human single-unit data available in the literature. Note,
70 however, that significant phase locking up to 7 kHz in chinchillas were obtained by Kale and Heinz
71 when averaging a lot of data to lower the noise floor of their recordings, thereby suggesting there
72 may still be usable temporal information even at these high frequencies (Verschooten et al.,
73 2019). A recent opinion paper on the use of phase locking cues in humans illustrates this
74 controversy: estimates of the highest frequency at which phase-locking information could be
75 used by humans ranged across “experts” in this field from 1.5 kHz to 10 kHz (Verschooten et al.,
76 2019).

77 One draw-back of using frequency-shifted inharmonic complex tones to investigate TFS
78 sensitivity is that these stimuli produce ambiguous pitch percepts and that subjects were not
79 explicitly asked to compare the pitches of inharmonic and harmonic complex tones; any audible
80 difference between the harmonic and inharmonic tones could be used as a cue. Furthermore,
81 harmonic and inharmonic complexes produce different envelopes at the output of a given
82 auditory filter which can potentially provide another cue to discriminate them. This led Moore &
83 Sek (2009) to randomize the starting phase of their components, which in turn affected the shape
84 of the stimulus envelope. Both this pitch ambiguity and the phase randomization may have an
85 impact on measures of TFS sensitivity and might impair subjects’ performance.

86 Here, we reexamine the TFS sensitivity of normal-hearing subjects using pulse spreading
87 harmonic complexes (PSHCs; Hilkuhysen & Macherey, 2014). PSHCs are harmonic complexes
88 whose phase relationship is tailored to manipulate the envelope rate independently from the f_0 .
89 In Experiment 1, we show that it is possible to produce two PSHCs that have the same long-term

spectrum, and identical envelopes but are perceived as either rising or falling in pitch across their duration, thereby avoiding the pitch ambiguity of inharmonic complexes. Acoustically, these stimuli only differ in their TFS. In Experiment 2, we use these stimuli to measure the lower limit of TFS sensitivity in different frequency regions and discuss the putative mechanisms underlying this limit.

Experiment 1: Pitch contour identification

Methods

Subjects and Equipment

Six normal-hearing subjects with ages ranging from 26 to 57 years (mean of 38.7) took part. Subject S4 was the author. They were seated in a double-walled sound proof booth in front of a computer screen. Stimuli were presented over an Etymotic ER2 earphone positioned inside one of their ears. The earphone was connected to a RME BabyFace Pro sound card. The experiment took place in the presence of a background noise that was played from a Zoom H4N recorder connected to the sound card.

Generation of PSHCs

The generation of PSHCs involves dividing the harmonics of a complex into several groups (called sub-complexes) and summing them separately before adding them back together with particular delays so that the overall envelope repetition rate remains regular across the stimulus duration. Following Hilkhuisen & Macherey (2014), a PSHC is defined by

$$s(t/k) = \sum_{i=M}^N \sin(2\pi f_0 i t + \varphi(i, k)) \quad (1)$$

where f_0 is the fundamental frequency, M is the lowest harmonic present, i is the harmonic number, N is the highest harmonic present, and t is the time. The starting phase of harmonic i is given by

$$\varphi(i, k) = 2\pi \frac{i}{k^2} r_j \quad (2)$$

where k is the PSHC order which determines the envelope repetition rate (equal to $k^2 f_0$) and j is defined as

$$j = (i \bmod k) + 1 \quad (3)$$

The mod operator indicates the remainder after division of i by k . Equation (3) assigns the i^{th} harmonic to the j^{th} sub-complex so that there are in total k sub-complexes. In our previous publications (Hilkhuisen & Macherey, 2014; Mesnildrey et al., 2015), r_j was a random element without replacement from $\{1, 2, \dots, k\}$ whose role was to spread the sub-complexes evenly across the stimulus period, presenting them in random order. Here, we consider two special cases of PSHCs where the sub-complexes are presented either in descending order (down-PSHC) or in ascending order (up-PSHC). For down-PSHC, r_j is given by

$$r_j = j \quad (4)$$

while for up-PSHC, it is given by

$$r_j = k - j + 1 \quad (5)$$

Stimuli

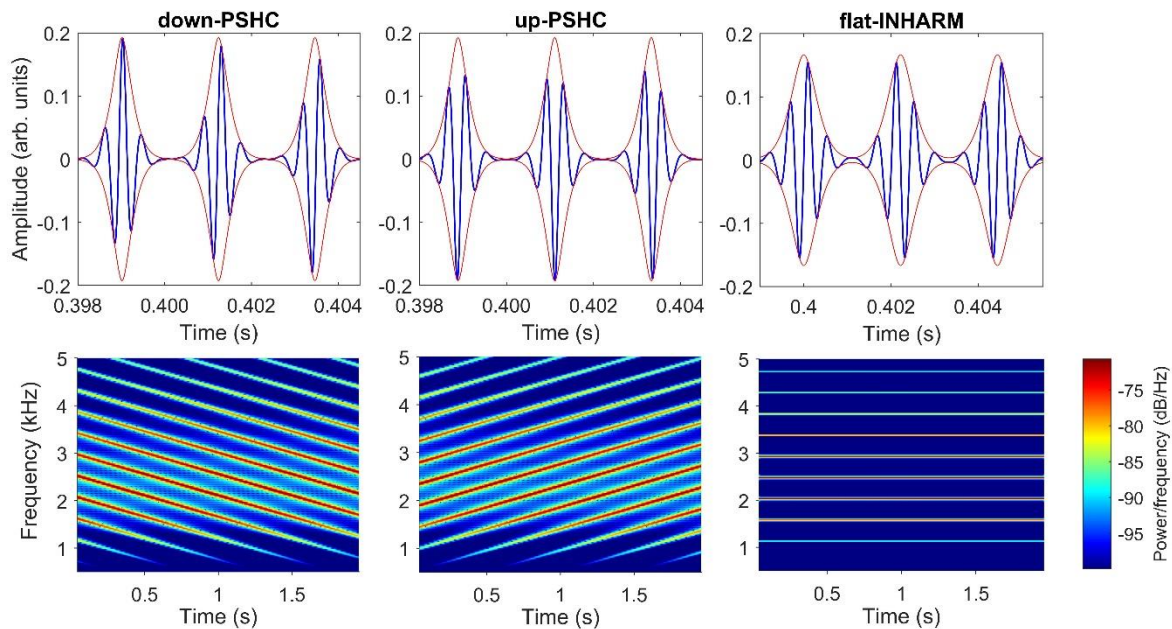
Stimuli consisted of up-PSHCs, down-PSHCs and inharmonic (INHARM) complexes synthesized in Matlab with a sampling rate of 96 kHz. Three versions of each of these stimuli were generated with envelope rates equal to 98 pulses per second (pps), 200 pps and 450 pps.

133 For the INHARM stimuli, the frequency components were randomly drawn with the constraint
 134 that the frequency separation between consecutive components was constant and equal to the
 135 envelope rate for each condition. For up- and down-PSHCs, the fundamental frequency was 2 Hz
 136 and the PSHC order k was 7, 10 and 15 for the three envelope rates, respectively.

137 All stimuli were bandpass filtered using a zero-phase 6th-order Butterworth filter (36 dB/oct.
 138 attenuation slopes) with -3-dB cut-off frequencies of 2000 and 2540 Hz, yielding a 2- ERB_N wide
 139 passband (Glasberg & Moore, 1990). The stimuli had a total duration of 500 ms (corresponding
 140 to a full period of the PSHCs) and were shaped with 20-ms raised-cosine onset and offset ramps.
 141 The PSHCs display gliding spectral ripples, as shown in Figure 1. For each presentation of the up-
 142 and down-PSHCs, the ripple starting phase varied randomly so that subjects could not identify
 143 the stimulus solely based on its onset or offset. The stimuli had an overall level 40 dB higher than
 144 the threshold in quiet of a pure tone with frequency corresponding to the middle of the passband.
 145 A continuous background of threshold-equalising noise (TEN) was presented at a level of 25 dB/
 146 ERB_N (same SNR as Moore & Sek (2009)).

147 The time waveforms and spectrograms of the three stimuli are shown in Figure 1 for an envelope
 148 rate of 450 pps. The blue curves in the top panels represent the time waveforms while the red
 149 curves show the Hilbert envelopes. At a given rate, the envelopes of the down- and up-PSHCs are
 150 identical but are slightly narrower and have a larger peak amplitude than the envelope of the
 151 INHARM complex (when compared at equal RMS). The spectrograms in the bottom panels show
 152 2-seconds of the three stimuli. The down- and up-PSHCs exhibit linear spectro-temporal ripples.
 153 The ripple density is determined by the envelope rate which corresponds to the frequency
 154 separation between adjacent ripples, while the ripple velocity is determined by the f_0 . Given that
 155 the PSHCs contain only harmonics of 2 Hz, they are both periodic, exactly repeating every 500 ms.
 156 The shallow-slope filters applied to the stimuli make them similar to continuous Shepard tones
 157 (referred to as “Risset glissando”) except that in our case the frequency separation between
 158 adjacent ripples is equal to a constant value in Hz whereas the components in Shepard tones are
 159 uniformly spaced on an octave scale (Shepard, 1964; Risset, 1969).

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162 Figure 1 — Top: In blue: temporal waveforms of three stimuli used in Experiment 1, all at a
 163 rate of 450 pps. The red line shows the Hilbert envelope. Only 3 envelope periods are shown.
 164 Bottom: Spectrograms showing 2 seconds of the same three signals.

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166 Procedure

167 The whole experiment was completed in one session lasting roughly an hour.

168 To determine the appropriate level of the complexes, the detection threshold was measured for
169 a 2254-Hz (geometric center of the passband), 500-ms pure tone using a three interval, three
170 alternative forced choice adaptive procedure with a 2-down, 1-up rule (c.f. Moore and Ernst,
171 2012). The signal level was adapted in steps of 8 dB until the second reversal, then in steps of 4
172 dB until the fourth reversal and finally in steps of 2 dB until the tenth reversal when the procedure
173 stopped. The threshold was calculated as the mean signal level at the last six reversals. Two
174 threshold estimates per subject were collected and their threshold was assumed to be the mean
175 of these two estimates. As previously mentioned, the overall level of the complexes and the level
176 of the background TEN used in the main part of the experiment were set at 40 dB and 25 dB/ERB_N
177 above this pure tone threshold, respectively.

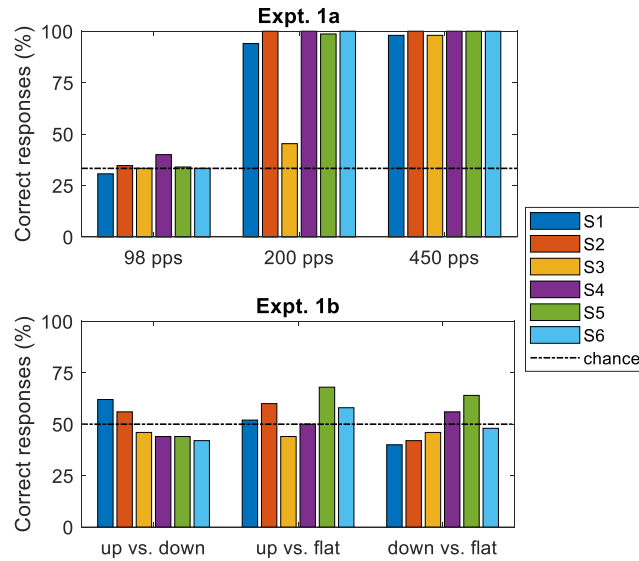
178 Experiment 1a used an identification task. On each trial, subjects heard one of the 9 stimuli (3
179 stimulus types x 3 envelope rates) and had to indicate whether they perceived the pitch as rising,
180 falling or staying constant across the 500-ms stimulus. Feedback was not provided. All stimuli
181 and envelope rates were presented in random order in blocks of 90 trials. Each subject performed
182 a total of 5 blocks, yielding 50 trials per stimulus in total.

183 In Experiment 1b, the same subjects took part in a three-interval two-alternative, “odd-man-out”
184 task to investigate whether they could discriminate between the up-PSHC, down-PSHC and
185 INHARM stimuli at the lowest envelope rate (98 pps). They were presented with a reference
186 stimulus in interval 1 followed by the same reference and a target stimulus randomly presented
187 in intervals 2 and 3. There were three different reference-target trials (up-PSHC vs. down-PSHC,
188 up-PSHC vs. INHARM and down-PSHC vs. INHARM). The trials were presented in blocks of 105,
189 consisting of 75 trials at 98 pps (25 trials for each condition) and 30 easier “catch” trials (5 trials
190 per condition for the two higher envelope rates). All subjects performed two blocks in total.
191 Feedback was provided.

192 Results

193 The top panel in Figure 2 shows the percent correct scores obtained in Expt. 1a for the six subjects
194 and the three envelope rates. Five out of six and six out of six subjects had scores higher than 92%
195 for envelope rates of 200 and 450 pps, respectively, showing that their perception was, at these
196 rates, consistent with expectations based on the time-frequency representations of the stimuli
197 (Figure 1). For the lowest rate (98 pps), however, all subjects performed at chance. Further
198 inspection of the data revealed that they perceived the stimuli to remain constant in pitch in 90%
199 of trials (i.e., for the three stimulus types), indicating that both the down- and up-PSHCs were also
200 perceived as constant in pitch.

201 The results of Expt. 1b (Figure 2, bottom panel) show that only S5 performed significantly above
202 chance for discriminating the inharmonic complex from each of the two PSHCs (up vs. flat and
203 down vs. flat conditions). However, none of the subjects could discriminate between the up- and
204 down-PSHCs. This shows that at 98 pps, subjects were not sensitive to TFS. It is possible that S5
205 used remaining envelope differences between the inharmonic tone and the PSHCs to perform the
206 task. The observation that he could not discriminate between the two PSHCs which had identical
207 envelopes would argue in favour of this explanation.



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Figure 2 — Top: Results of Expt. 1a showing the percentage of correct identification at each of the three envelope rates for each subject. Bottom: Results of Expt. 1b showing the percentage of correct discrimination of the three pairs of stimuli for each subject.

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Discussion

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The results of Experiment 1 show that, for a given passband, there is an envelope rate below which down- and up-PSHCs cannot be discriminated and are not being perceived as changing in pitch. Below we describe the cues that the subjects may have used to perform the pitch contour identification task of Expt. 1a and discuss the possible reasons why their performance got poorer at the lowest envelope rate. These cues are excitation pattern cues and phase locking cues.

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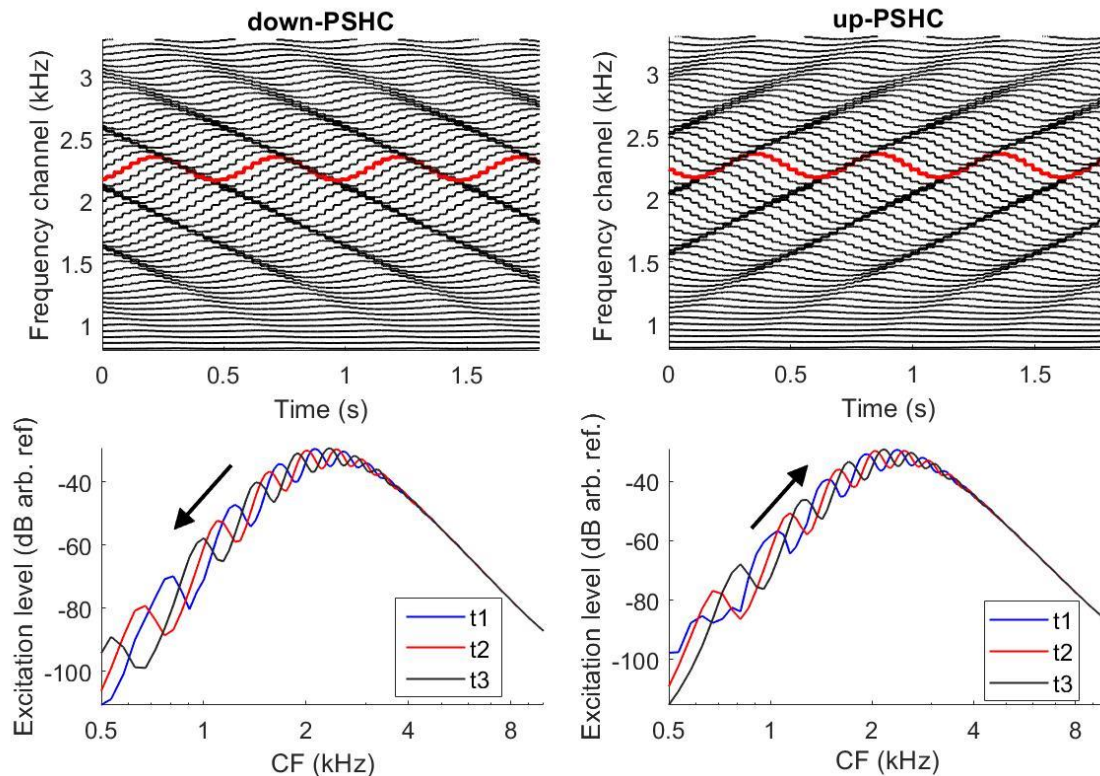
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The top panels of Figure 3 show simulations of basilar membrane vibrations using a Gammatone filterbank (Slaney, 1998) in response to 2-seconds of 450-pps envelope rate, down- and up-PSHCs in the absence of the background TEN. Each line represents the evolution of the RMS value of a certain auditory filter output (whose characteristic frequency is indicated on the y axis) computed across successive periods of the envelope. There is a clear amplitude modulation at the output of all filters at a frequency equal to the fundamental frequency (2 Hz). The starting phase of this modulation is, however, different across filters so that at any given time, some filters have a high amplitude and others have a low amplitude. This is illustrated in the bottom panels of Figure 3 which show excitation patterns calculated across a single envelope period at three successive times across the stimulus. These excitation patterns represent the RMS outputs of the Gammatone filters expressed on a dB scale. All excitation patterns show peaks separated by a frequency equal to the envelope rate. However, the peaks drift during the stimulus period. For the down-PSHC, the peaks shift progressively downwards across the stimulus duration while for the up-PSHC, they shift upwards. The perception of down-PSHCs as falling in pitch and of up-PSHCs as rising in pitch may reflect the use of excitation pattern cues in two different ways: Subjects may either selectively attend a particular peak in the excitation pattern and follow its course across the stimulus duration or they may perceive a continuously changing residue pitch based on the continuous analysis of the pattern of peaks present in the excitation pattern (e.g., using a pattern-matching mechanism based on central templates; c.f. Terhardt, 1974). When the envelope rate is decreased, this has the effect of increasing the ripple density and, therefore, reducing the size of the peaks in the excitation pattern. This is similar to what happens when decreasing the f_0 of a harmonic complex filtered in a fixed frequency region: the peaks in the excitation pattern get smaller and smaller as the harmonics become less and less resolved. This may, therefore, explain why the identification task was impossible at 98 pps.



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Figure 3 — Top: RMS energy at the output of several Gammatone filters in response to down- and up-PSHCs with an envelope rate of 450 pps. The RMS energy was calculated across successive envelope periods. The red function corresponds to the filter located in the center of the passband (2254 Hz). Bottom: Excitation patterns at three successive times (t1, t2 and t3) during a period of the stimulus for the same signals.

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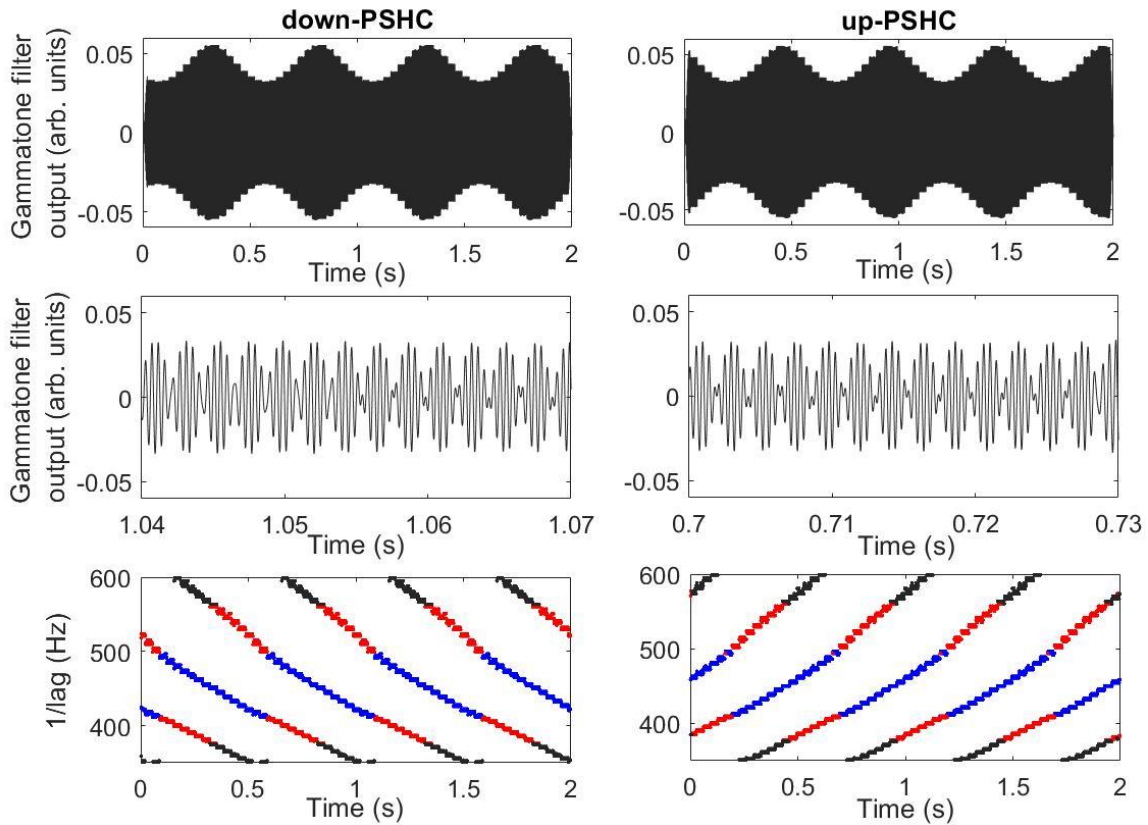
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The second potential mechanism is temporal. The top panels of Figure 4 show the output of an auditory filter centred on 2254 Hz over 2 seconds (4 periods of the f_0) for both PSHCs. The similarity between the outputs obtained for the two PSHCs suggest that there is no information in the envelope at the output of a given auditory filter that can allow the identification of the pitch contour. The middle panels of Figure 4 show a few envelope periods of these same signals. It can be observed that the TFS changes from one envelope period to the next. To quantify this change and to determine the time intervals conveyed by the TFS peaks, the auditory filter output waveform of the first envelope period of the stimulus was cross-correlated with the output waveform of the second envelope period. The lags corresponding to the first three maxima of the cross-correlation function were stored. Then, the second period was cross-correlated with the third period and so on until the end of the stimulus. The bottom panels of Figure 4 show the reciprocal of the lags corresponding to the three highest peaks of these cross-correlation functions as a function of time. These values can be viewed as the possible “pitches” conveyed by the TFS peaks at the output of this specific filter at any given time. This analysis shows that the TFS information *within* a single auditory filter provides a cue that may allow subjects to perceive the pitch contour of down- and up-PSHCs because the reciprocal of the distance between the TFS peaks progressively decreases for down-PSHC and progressively increases for up-PSHC. However, these TFS variations are still present at low envelope rates (not shown here), including at 98 pps where subjects could not do the task. Therefore, to explain why performance is getting worse at low rates, we also need to assume that there is a frequency-dependent temporal limitation on the time intervals that can be analyzed by the central auditory system to extract pitch, as already proposed in previous publications (Moore, 1982; Pressnitzer et al., 2001).



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Figure 4 — Top panels: Output of a gammatone filter centered on 2254 Hz (center of the passband) for the two PSHCs. Middle panels: Short portions of the same output showing the TFS. Bottom panels, Reciprocal of the lags corresponding to the three highest peaks of the cross-correlation function between one envelope period and the next. Blue, red and black symbols are for the highest, second-highest and third-highest peaks, respectively.

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Experiment 2: Measuring the lower limit of TFS sensitivity

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Methods

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Subjects

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Stimuli

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The stimuli were down- and up-PSHCs of various envelope rates filtered into seven different frequency regions. The filtering was identical to that for Expt. 1 except that F_c was equal to 0.25, 0.5, 1, 2, 4, 8 or 11.2 kHz depending on condition. The upper cut-off frequency was set so that the passband width would always be equal to 2 ERB_N . The overall presentation level of the complexes was again 40 dB higher than the pure tone detection threshold for a frequency corresponding to the centre of the passband and the level of the TEN noise was 25 dB/ ERB_N above the detection threshold. Because we did not measure the thresholds in the middle of each passband, this reference threshold was obtained by interpolation from the threshold measurements made for the different values of F_c .

296 **Procedure**

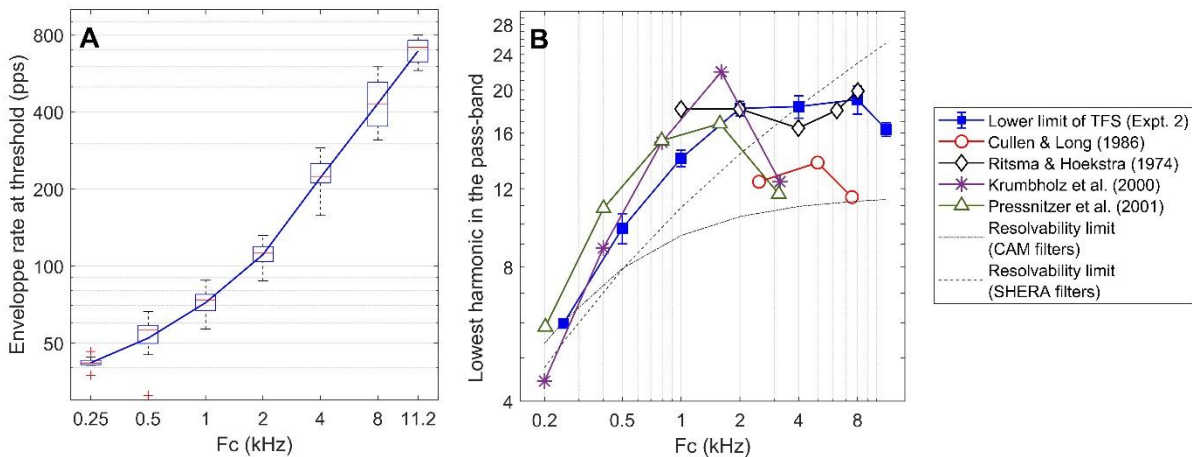
297 The main task was a 3I2AFC, 2-down, 1-up adaptive task. In the first interval, the subjects always
 298 heard the down-PSHC. In intervals 2 and 3, the up-PSHC and down-PSHC were presented in
 299 random order. Subjects had to indicate which stimulus was different than the other two. The three
 300 stimuli presented in each trial had the same envelope rate, so subjects could only use differences
 301 in TFS to do the task. The starting envelope rate was equal to $0.2F_c$. Following two correct
 302 responses, the envelope rate was divided by $(1.05)^\alpha$ while following one incorrect response, it
 303 was multiplied by $(1.05)^\alpha$. α was equal to 4 until the second reversal, then it was switched to 2
 304 until the fourth reversal and finally to 1 until the tenth reversal at which point the procedure
 305 stopped.

306 While we aimed to use the same f_0 of 2 Hz for all stimuli, this was not always possible because, for
 307 a given f_0 , the envelope rate can only be equal to $k^2 f_0$ where k is an integer and can therefore only
 308 take a finite number of values. Therefore, the f_0 value closest to 2 Hz was selected for each desired
 309 envelope rate. This means that the f_0 could slightly vary from trial to trial (from 1.7 to 2.4 Hz in
 310 the lowest frequency region and substantially less in higher frequency regions). Note, however,
 311 that the f_0 was constant *within* a trial and could not be used as a cue to perform the task.

312 A measurement block involved collection of seven discrimination threshold measurements, one
 313 for each frequency region, presented in random order. Subjects performed between 5 and 6
 314 blocks in total and the first block was considered as training and was not taken into account in
 315 the analyses. This experiment was completed in two sessions of 2 hours.

316 **Results**

317 Figure 5A shows the discrimination thresholds (i.e. reflecting the lower limit of TFS sensitivity)
 318 obtained as a function of F_c . The lower limit of TFS significantly increased with increases in F_c ,
 319 ranging from 42 pps for $F_c=0.25$ kHz to 691 pps for $F_c=11.2$ kHz. Except for one subject whose
 320 threshold was lower at 0.5 than at 0.25 kHz, all subjects showed a monotonic increase as a
 321 function of F_c .



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323 Figure 5 — A: Boxplots showing the distributions of the lower limit of TFS sensitivity for each
 324 F_c . Each boxplot shows the median, 25th and 75th percentiles and extreme values. Outliers (red
 325 '+' symbols) correspond to values that are more than 1.5 times the interquartile range away
 326 from the bottom or top of the box. The solid line shows the mean across subjects. B, The same
 327 data as in panel A are plotted in blue as a function of the lowest virtual harmonic in the
 328 passband (see main text). The dashed and dashed-dotted lines show the limit of harmonic
 329 resolvability for two sets of auditory filters (see main text for the definition of resolvability).
 330 The other functions illustrate transition rates from good to poor frequency discrimination for
 331 harmonic complex tones, replotted from Krumbholz et al. (2000).

332 The solid blue line connecting the filled squares in Figure 5B shows the same data expressed as
 333 the ratio between F_c and the lower limit of TFS. We refer to this dimensionless variable as the
 334 rank of the lowest *virtual* harmonic present in the passband “ N_{LOW} ” at threshold as it represents
 335 the rank of the lowest-frequency ripple present in the passband. A one-way ANOVA showed a
 336 significant effect of F_c on N_{LOW} ($F(6,54)=43$, $p<0.001$). Paired t-tests (without correction for
 337 multiple comparisons) performed on the data obtained for successive values of F_c showed that
 338 N_{LOW} increased significantly from 0.25 to 0.5 kHz ($p=0.001$), from 0.5 kHz to 1 kHz ($p=0.003$) and
 339 from 1 kHz to 2 kHz ($p<0.001$), remained approximately constant from 2 to 8 kHz and finally
 340 decreased from 8 to 11.2 kHz ($p=0.042$). Interestingly, the across-subject mean N_{LOW} value was
 341 higher than 18 for $F_c=2, 4$ and 8 kHz and was still higher than 16 for $F_c=11.2$ kHz. These large
 342 N_{LOW} values suggest that the ripples were spectrally unresolved in the passband according to
 343 usual definitions of resolvability (Moore & Gockel, 2011).

344 Discussion

345 As previously explained, our subjects may have used either excitation pattern or phase locking
 346 cues to perform the tasks in the two experiments. If subjects based their judgments on excitation
 347 pattern cues, we would expect the lower limit of the use of TFS to depend on the bandwidths of
 348 the auditory filters. The dashed line of Figure 5B illustrates the limit of harmonic resolvability as
 349 defined by Moore & Ohgushi (1993); components separated by less than $1.25ERB_N$ are assumed
 350 to be unresolved. This limit falls below the lower limit of TFS sensitivity for all regions except the
 351 lowest, suggesting that, at threshold, the ripples of our stimuli were unresolved. The dash-dotted
 352 line also shows the same “resolvability” limit, but using ERB values proposed by Shera et al.
 353 (2002), which are smaller at high frequencies. These ERB values likely represent a conservative
 354 definition of resolvability given that they were obtained at lower levels than used here (Oxenham
 355 & Simonson, 2006). For $F_c<4$ kHz, the lower limit of TFS still falls above this line, confirming that
 356 the ripples at threshold were unresolved even assuming narrow auditory-filter bandwidths. For
 357 $F_c>4$ kHz, it cannot be excluded that the ripples were partially resolved. However, if the subjects
 358 based their judgments on excitation pattern cues, we would expect N_{LOW} for the lower limit of TFS
 359 sensitivity to continue to increase up to the highest F_c . This was not the case as N_{LOW} remained
 360 mostly constant above 2 kHz. Also, it should be noted that the random fluctuations produced by
 361 the background TEN should reduce the ability to use excitation-pattern cues (Jackson & Moore,
 362 2014). Thus, unless our subjects managed to use residual excitation pattern cues in the lower
 363 skirt of the filter, these data suggest that the lower limit of the use of TFS is related to the use of
 364 temporal (phase-locking) cues rather than excitation-pattern cues.

365 Moore et al. (2009) measured sensitivity to TFS for several f_0 values in different frequency
 366 regions. They showed that for stimuli bandpass filtered so that the lowest component in the
 367 passband, N_{LOW} , was harmonic 13, subjects could discriminate harmonic and inharmonic tones
 368 for $f_0=50, 100$ and 200 Hz. At these f_0 , harmonic 13 corresponds to $F_c=1.3, 2.6$ and 5.2 kHz,
 369 respectively. Our results are consistent with their data because at these F_c values, our subjects
 370 could always discriminate between down- and up-PSHCs when N_{LOW} was the 14th or lower (see
 371 Figure 5B). They also showed that subjects required the presence of lower harmonics to perform
 372 the same task for $f_0=35$ Hz. Similarly, Figure 5B shows that our N_{LOW} was lower in low frequency
 373 regions. Tarnowska et al. (2019) showed above-chance performance for musicians on a variant
 374 of the TFS task used in Moore et al. (2009) for $F_c=3.8$ kHz and $N_{LOW}=19$ which is also consistent
 375 with the present data. Finally, Moore & Sek (2009) extended these measurements to higher
 376 fundamental frequencies ($f_0=800$ and 1000 Hz) and showed sensitivity to TFS when N_{LOW} was
 377 equal to 12 although only 6 out of their 8 subjects could perform the task at the highest f_0 . Their
 378 stimuli are equivalent to $F_c=9.6$ and 12 kHz, respectively, and can be compared to our highest-
 379 frequency region ($F_c=11.2$ kHz) for which subjects could discriminate down- and up-PSHCs for
 380 $N_{LOW}=16$ and lower. It is possible that the poorer performance Moore & Sek (2009) observed for
 381 $F_c=12$ kHz than for $F_c=9.6$ kHz is related to the degradation of phase locking cues at very high
 382 frequencies. The trend of decreased performance we observed in the highest frequency region
 383 may have the same origin.

384 In summary, the finding that subjects were still sensitive to TFS when N_{LOW} was equal to 18 for
 385 $F_c=2, 4$ and 8 kHz suggests that the ripples were unresolved and that subjects used temporal cues
 386 to perform the task. These results, therefore, confirm the findings of Moore & Sek (2009) and add
 387 further evidence that phase locking cues can be used by humans at very high frequencies.

388 Finally, it has been shown that the frequency discrimination of harmonic complex tones depends
 389 on the rank of the lowest harmonic present in the passband. When the frequency region is fixed,
 390 f_0 difference limens (DLs) are poorer at low than at high f_0 (Ritsma & Hoekstra, 1974; Cullen &
 391 Long, 1986; Krumbholz et al., 2000). The transition from good to poor performance, however,
 392 depends on frequency region. Krumbholz et al. (2000) compiled the results of several of these
 393 studies (c.f. their Figures 7 and 10) and defined the transition rate as the rate at which the f_0 DL
 394 equals 2.5% except for the Ritsma and Hoekstra (1974) data for which the criterion was set to
 395 1%. These transition rates, expressed in terms of the rank of the lowest harmonic number in the
 396 passband are replotted in Figure 5B. The upward triangles also show the lower limit of melodic
 397 pitch defined as the rate at which subjects could no longer recognize that the f_0 of a complex tone
 398 in a melody changed by a semitone (Pressnitzer et al., 2001). The functions showing these
 399 transition rates as a function of F_c follow a similar pattern as the lower limit of TFS, first showing
 400 an increase followed by a decrease or a flat portion above 1 kHz. Although speculative, it is
 401 possible that the transition from good to poor f_0 discrimination of complex tones with increasing
 402 harmonic rank reflects the decreased sensitivity to TFS in high-frequency regions.

403 Conclusions

404 These experiments show that it is possible to generate pairs of harmonic complexes that share
 405 the same long-term spectrum and the same temporal envelope but have different TFS and elicit
 406 different pitch percepts. These down- and up-PSHCs add to the arsenal of tools for studying
 407 sensitivity to TFS. The lower limit of TFS sensitivity (expressed as the envelope rate below which
 408 subjects were insensitive to TFS) was shown to increase with increasing frequency region. The
 409 observation that subjects were still sensitive to TFS in high frequency regions (> 4 kHz) when the
 410 stimuli likely contained only unresolved components suggests that phase locking cues remain
 411 usable at high frequencies, confirming the results of previous studies.

412 Acknowledgements

413 I thank Bob Carlyon and Brian Moore for their comments on a previous version of this manuscript.

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