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1 **On the variation of interaural time differences with frequency**

2 Victor Benichoux^{a)b)} and Romain Brette^{a)}

3 *Institut de la Vision,*

4 *(INSERM U968,*

5 *CNRS UMR 7210,*

6 *UMR S 968)*

7 *17,*

8 *rue Moreau*

9 *75012 Paris,*

10 *France*

11 Marc Rébillat

12 *PIMM,*

13 *Arts et Métiers ParisTech - CNRS - CNAM,*

14 *151,*

15 *Boulevard de l'Hopital*

16 *75013 Paris,*

17 *France*

18 (Dated: February 15, 2016)

^{a)} Also at: Institut d'Etudes de la Cognition, Ecole Normale Supérieure, Paris, France

Abstract

Interaural time difference (ITD) is a major cue to sound localization in humans and animals. For a given subject and position in space, ITD depends on frequency. This variation is analyzed here using an HRTF database collected from the literature and comprising human HRTFs from 130 subjects and animal HRTFs from six specimens of different species. For humans, the ITD is found to vary with frequency, in a way that shows consistent differences with respect to a spherical head model. Maximal ITD values were found to be about $800 \mu\text{s}$ in low frequencies and $600 \mu\text{s}$ in high frequencies. The ITD variation with frequency (up to $200 \mu\text{s}$ for some positions) occurs within the frequency range where ITD is used to judge the lateral position of a sound source. In addition, ITD varies substantially within the bandwidth of a single auditory filter, leading to systematic differences between envelope and fine-structure ITDs. Because the frequency-dependent pattern of ITD does not display spherical symmetries, it potentially provides cues to elevation and resolves front/back confusion. The fact that the relation between position and ITDs strongly depends on the sound's spectrum in turn suggests that humans and animals make use of this relationship for the localization of sounds.

20 I. INTRODUCTION

21 In humans and many animals, a major cue to localize sounds in the horizontal plane is
22 the difference in time between the peaks and valleys of the acoustical wave at the two ears, i.e.
23 the interaural time difference (ITD). Remarkably, humans can distinguish ITD differences
24 as low as $20 \mu\text{s}$ for a wide array of sound spectra and envelope characteristics below about
25 1.5 kHz (Mills, 1958; Brughera *et al.*, 2013). Furthermore, ITD has been shown to have a
26 stronger influence than interaural level differences (ILD) on the perceived lateral location of
27 sounds with energy in low frequencies (below 2.5kHz, (Wightman and Kistler, 1992)). In
28 animals as well, ITD is used as a cue to sound location: cats, gerbils, birds, reptiles and
29 others have dedicated neural structures in the auditory brainstem to process ITD (Grothe
30 *et al.*, 2010). Understanding the neural processing of ITDs requires a precise knowledge of
31 the nature of the temporal disparities imposed by the head, body and environment.

32 The relationship between source position and ITD is constrained by morphological pa-
33 rameters including the interaural distance, head, ear position, shape, torso, and (even)
34 hair (Duda *et al.*, 1999; Algazi *et al.*, 2001b). Measuring ITDs for tones using a manikin,
35 Kuhn (1997) found that the ITD also varies systematically with the frequency of the tone,
36 as reproduced in Fig. 1a. The ITD for a 2000 Hz tone presented at 45° is $400 \mu\text{s}$ (Fig. 1a,
37 dashed line), while the ITD for a 500 Hz tone at the same position is $600 \mu\text{s}$ — about
38 50% larger. Conversely, sounds presented at different positions can produce the same ITD,
39 provided they have different frequency contents. It follows then that spatial position cannot
40 be estimated from ITD independently of sound frequency. This physical phenomenon is
41 known, and has been observed in models where the head is a rigid sphere (Kuhn, 1977),
42 or an ellipsoid (Cai *et al.*, 2015). As an illustration we computed ITDs from the spherical
43 head model (details below) using a head radius of 9.3 cm (as reported in (Kuhn, 1977)), and
44 plotted it on Fig. 1b.

45 Despite these early insights, the dependence of ITD on frequency in humans and animals
46 has not, to our knowledge, been quantitatively examined. We propose here to bridge that

b)Electronic address: `victor.benichoux@ucdenver.edu`

47 gap by a careful and in-depth assessment of the frequency-dependence of ITD in human and
 48 animal acoustical data. Furthermore, we provide a new interpretation of this dependence,
 49 showing that it results in different ITDs in the envelope and fine-structure of auditory filters’
 50 outputs.

51 After a review of the physics of the frequency-dependence of ITD using previous reports
 52 of the spherical model (section II), we provide a quantitative analysis of this phenomenon
 53 in acoustical recordings of 130 subjects from four databases (section III). Further, we show
 54 that ITDs between the envelopes and fine-structures of binaural signals are different (section
 55 IV). Finally, we analyze the frequency-dependence of ITDs in the HRTFs of six different
 56 animal species (section V), and show that the highly non-spherical nature of many animals’
 57 heads makes it hard to predict the range of ITD from head size.

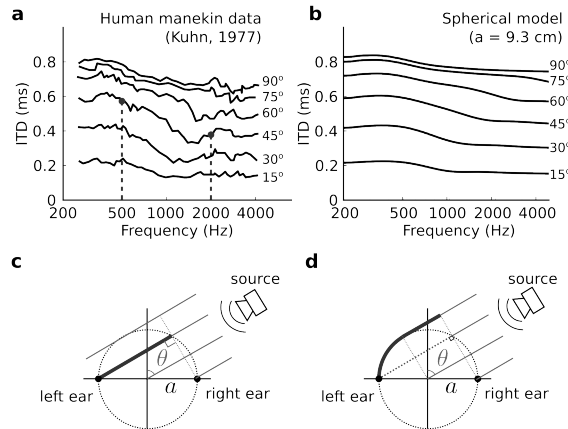


Figure 1: Frequency-dependence of ITD. (a) ITD measured with pure tones of varying frequency for different source positions on a human manikin (replotted from Kuhn (1977)). (b) ITD computed for a spherical head model with head radius 9.3 cm. (c) Propagation of a planar sound wave with an acoustically transparent head. The additional pathlength to the contralateral ear (thick line) is a sine function of the azimuth angle θ . (d) Propagation of a high frequency planar sound wave diffracted by a sphere. The additional path to the contralateral ear is the thick line.

58 II. SCATTERING AND FREQUENCY-DEPENDENT ITDS

59 A. Phase ITD

The complete acoustical transformation occurring between a point source and the ears of a subject can be modeled as a pair of filters (H_L, H_R) usually termed Head Related Transfer Functions (HRTFs). The *phase ITD* (ITD_p , as reported in the original (Kuhn, 1977) study), is the ITD of the fine-structure of the binaural signal, defined at any frequency f using the phase response of the HRTFs:

$$\text{ITD}_p(f, \theta, \phi) = \frac{1}{2\pi f} \angle \left[\frac{H_L(f, \theta, \phi)}{H_R(f, \theta, \phi)} \right] \quad (1)$$

60 where θ is azimuth measured in radians, ϕ is elevation (in standard vertical-polar coordinates:
61 azimuth between -180° and 180° , and elevation between -90° (down) and 90° (up)). The
62 bracket operator \angle is the *unwrapped phase* operator that yields a continuous phase spectrum
63 (not constrained to $[-\pi, \pi]$). By convention, positive azimuth values indicate that the source
64 is to the right of the subject, where ITD_p is positive.

65 B. ITD in the spherical head model

66 In a first, simplified geometrical model of ITD, we can consider a planar acoustical
67 wave incident on an acoustically transparent head (Figure 1c). In this case, the ITD is
68 the difference in path lengths to the two ears (thick line) divided by the speed of sound:
69 $\text{ITD}(\theta) = 2\frac{a}{c} \sin(\theta)$, where θ is the azimuth of the sound source, c the speed of sound in air
70 and a the head radius. In this description, ITD does not depend on frequency: ITD does
71 show frequency dependence because the head is not acoustically transparent.

72 A more plausible acoustical model of the situation is to assume that the head is a rigid
73 sphere, with ears lying on a diameter. The first observation that ITD is frequency-dependent
74 in this context is attributed to Lord Rayleigh's spherical head model (Rayleigh and Lodge,
75 1904). Many studies have then used this model to analyze binaural cues (Duda and Martens,
76 1998; Kuhn, 1977). In particular, the phase ITD, i.e. ITD_p as defined in Eq. 1, can be

77 numerically calculated at all frequencies for the spherical head model, as shown on Fig. 1b
 78 (for sources at infinite distance from the head, following Bruneau (2010)). In this model,
 79 ITD_p for any given source position generally decreases with increasing frequency (Fig. 1b),
 80 which is broadly consistent with the human manikin data reported by Kuhn (1977) and
 81 shown in Fig. 1a.

For high frequencies, when the wavelength is small compared to the head radius, the ITD tends to the difference between the shortest path lengths to the two ears divided by the speed of sound (thick line in Figure 1c), which is expressed in Woodworth’s formula:

$$ITD_{HF}(\theta) = \frac{a}{c}(\sin(\theta) + \theta) \quad (2)$$

The low-frequency limit of ITD can be calculated by considering the first terms in the spherical-harmonic development of the acoustical field solution (Kuhn, 1977):

$$ITD_{LF}(\theta) \approx 3\frac{a}{c}\sin(\theta) \quad (3)$$

82 The ratio between low and high frequency ITD is then: $\frac{3\sin(\theta)}{\theta+\sin\theta}$, which is always greater than
 83 one. Thus the the low-frequency ITD is always greater than the high frequency ITD. For
 84 azimuths θ between 0 and $\pi/2$ radians (90°), this ratio is a monotonically decreasing function
 85 of θ . For sources near 0° , the ITD is 50% larger at high frequency relative to low frequency,
 86 but for those positions (close to the midline) ITD values are close to zero. Conversely, when
 87 the ITD is maximal for azimuths near 90° , the low frequency ITD is only about 16% larger
 88 than the high frequency ITD. Readers should note that this is hard to see on 1b.

89 C. Visualization of the scattering phenomenon

90 At low frequency, the head is small compared the wavelength of the sound, and one
 91 might infer that the ITD should be close to the situation when the head is acoustically
 92 transparent (Fig. 1c). This would predict a smaller ITD than in high frequency, yet the
 93 opposite occurs. The reason for this counter-intuitive phenomenon is that the sphere is not
 94 an obstacle between the source and the ears, but rather the ears are *on* the sphere and
 95 diffraction phenomena are at play (Kuhn, 1977).

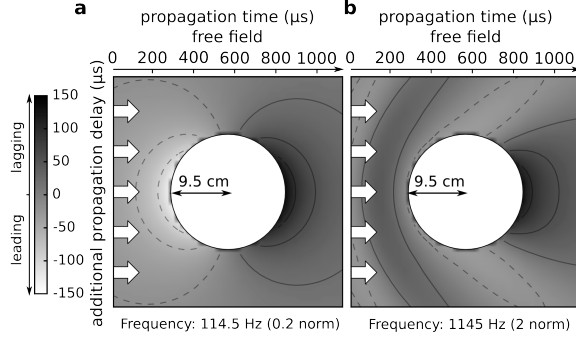


Figure 2: Propagation time of a planar sound wave in the presence of a sphere, relative to the propagation time in free field, for tone frequencies 114.5 Hz (a) and 1145 Hz (b). Propagation time in free field (no head) is shown on top. Negative values (lighter shades) indicate regions where phase is leading, and positive values (darker shades) indicate regions where the sound phase is lagging.

96 To get a better grasp of the situation, we calculated and represented the acoustical field
 97 in the vicinity of the head, using the formula in Bruneau (2010, paragraph 5.2.3). In Fig. 2,
 98 we show the steady-state propagation time of a monochromatic planar wave emanating
 99 from an infinite-distance source to the left ($\theta = 90^\circ$), relative to the propagation time for
 100 an acoustically transparent head (free field). For head radius of 9.5 cm, the free field ITD
 101 is about $550 \mu\text{s}$. For a low frequency tone (about 115 Hz, Fig. 2a), a phase lead appears on
 102 the ipsilateral side of the head (the acoustical wave is “compressed” against the head), and
 103 a phase lag appears on the contralateral side (the wave must turn around the head). As a
 104 result, the ITD is $550 + 150 + 150 = 850 \mu\text{s}$. For a high-frequency tone (1145 Hz, Fig. 2b),
 105 the propagation time to the ipsilateral ear (left) is not affected by the head but there is
 106 still a phase lag at the contralateral ear, corresponding to the additional path length. As a
 107 result, the ITD is $550 + 150 = 700 \mu\text{s}$, which is smaller than at low frequency.

108 The physical phenomenon is entirely specified by the wavelength ($\lambda = c/f$) of the
 109 acoustical wave relative to the size of the sphere. To account for the effect of the size of the
 110 head, it is thus convenient to introduce a normalized frequency scale, where unit normalized

111 frequency ($f_{norm} = 1$) corresponds to the physical frequency of a wave with wavelength
112 equal to one sphere circumference: $f = c/2\pi a$. Scaling head size also scales ITD (it is
113 inversely related), and therefore ITD can also be normalized, so that a scaled ITD of unity
114 ($ITD_n = 1$) corresponds to a physical ITD of a/c , the time for sound to propagate one
115 radius of the spherical head. Assuming a head radius of $a = 9.5$ cm, the low-frequency
116 condition of Fig. 2 corresponds to a normalized frequency of 0.2, and the high-frequency
117 condition to a normalized frequency of 2.0.

118 From this description, in terms of normalized time and frequency, the effect of changing
119 the head size on $ITD_p(f)$ is easier to grasp. It is two-fold: for a given normalized frequency,
120 the ITD depends linearly on head size; and the frequency scale on which ITD varies depends
121 linearly on the inverse of head size. In particular, the transition between the low and high
122 frequency regimes occurs at lower frequencies for bigger head sizes.

123 III. FREQUENCY-DEPENDENCE OF ITD IN HUMAN HRTFS

124 Human head morphology is more complex than a sphere, and other parts of the human
125 body also influence the ITD (Kuhn, 1977). Furthermore, comparing the human-manikin
126 ITDs to the spherical-head ITDs in Fig. 1a-b reveals that ITDs exhibit a more complex
127 frequency-dependence in humans than in the spherical head model. Therefore it is necessary
128 to analyze the frequency-dependence of ITD from HRTF measured in real human subjects.

129 A. HRTF databases

130 HRTF data were obtained from three publicly available databases (ARI (ARI, 2010),
131 CIPIC (Algazi *et al.*, 2001a) and LISTEN-V1 (Warusfel, 2002)). Another set of data was
132 specifically recorded for this project (LISTEN-V2), following the protocol of the LISTEN-V1
133 database, and has not been made public yet. All data are available from the corresponding
134 author on request. Overall, this combined dataset includes 130 subjects (Table I). Because
135 these databases were obtained in slightly different conditions (in particular spatial measure-

136 ment grids and number of samples), ITDs were evaluated separately in each database, and
137 then all statistics were interpolated on a common space-frequency grid (that of LISTEN-V2)
138 using a natural neighbor interpolation. Results are therefore always presented with a spatial
139 resolution of 5° in azimuth and about 15° elevation.

140 **B. Frequency dependence of human ITDs**

141 *1. Acoustical head radius estimation and normalization*

142 As discussed above, the subject’s head size affects ITD across positions and frequencies
143 in a way that is completely predicted by the acoustics of sound propagation. We are not,
144 however, interested in the variability of ITD cues across the population of subjects that
145 is explained by head size. Rather, we are interested in how this variability reflects the
146 variability in head morphologies. Furthermore, increasing headsize systematically shrinks
147 the frequency axis, thus averaging different subjects’ ITD at each frequency will spuriously
148 smooth out ITD variations. Therefore, in order to account for the effect of head size across
149 the population of subjects, we normalize the time and frequency axes of each subject’s
150 ITD data using a measure of the head of the subject derived from its HRTFs (usually
151 termed *acoustical head radius*, e.g. in (Algazi *et al.*, 2001b)). Similar normalization methods
152 have been proposed in the context of reducing variability in spectral notches position and
153 amplitude (Middlebrooks, 1999).

154 We define the “acoustical head radius” for each subject as the radius of the spherical
155 model which best matches the subject’s high-frequency ITD. More precisely, for each subject
156 we compute the high frequency ITD at all positions as the average phase ITD between 3kHz
157 and 5kHz. We compute the spherical-model high-frequency ITDs in the exact same way
158 and for the same positions. The radius of the sphere is then adjusted so as to minimize the
159 squared differences between the subject’s ITDs and the sphere’s. This regression is performed
160 using a standard gradient-descent algorithm. The best-fitting sphere radius resulting from
161 this procedure is the *acoustical head radius* of the subject. We validated this method by

162 simulating HRTFs using the spherical head model, and recovering the radius of the simulated
163 spherical head. As expected, we found that this method estimated accurately the radius of
164 the sphere within 0.01 mm (over a range of sphere radii from 5cm to 15 cm).

165 We then estimated the acoustical head radius of each subject in the population. We
166 found the average head radius over all subjects to be 9.5 cm (N=130, ± 0.48 cm standard
167 deviation, 8.3 to 10.8 cm range). For each subject, we computed the mean squared error
168 between ITDs derived from the optimal spherical model and acoustically measured ITDs.
169 The mean squared error was on average $67 \mu\text{s} \pm 22 \mu\text{s}$ STD across the population, indicative
170 of a consistently good fit. The average head radius value we found is slightly higher than
171 the one reported in the (Algazi *et al.*, 2001b) study, which was obtained using another ITD
172 estimation method (onset-time differences), and only on positions on the horizontal plane.
173 The same estimation and fitting method on our data yields a radius of 8.43 cm (± 1.14 cm),
174 consistent with the value reported by (Algazi *et al.*, 2001b).

175 The goal of this normalization procedure was to account for the systematic effect of
176 head size on the variability of the ITD measures across the population. We computed the
177 standard deviation of ITD at each frequency and position across the population of subjects
178 before and after normalization. The average standard deviation before normalization was 54
179 μs and reduced by about 20% with normalization (42 μs STD, using the average head size
180 of 9.5 cm to convert to physical units). This reduction was quantitatively different across
181 databases, and more pronounced in databases with more subjects (45% in LISTEN-V2).

182 Most ITDs and derived statistics are reported in the rest of the manuscript on *normalized*
183 frequency and ITD scales with a single pair of normalization factors (frequency and ITD)
184 for the population. For ease of reading, when representing human ITD data, ITDs and
185 frequencies are represented both in normalized and direct physical units, with a conversion
186 factor assuming a head radius equal to the average over the population ($a = 9.5$ cm). For
187 this value of the head radius, a normalized frequency of 1 corresponds to a frequency of 573
188 Hz, and a normalized ITD of 1 corresponds to an ITD of 278 μs . Therefore, to convert from
189 normalized to physical ITD in μs , multiply the normalized value by 278 μs . To convert from

190 normalized to physical frequency, multiply the normalized value by 573 Hz.

191 *2. Asymptotic ITD in the horizontal plane*

192 We estimated the asymptotic low and high frequency values of the ITD to compare them
193 with theoretical predictions from the spherical model (Figure 3).

194 The high-frequency ITD, $\text{ITD}_{\text{HF}}(\theta)$ is estimated as the mean ITD between $f_{\text{norm}} = 7$
195 (4010 Hz) and $f_{\text{norm}} = 8$ (4600 Hz). As per construction, the Woodworth formula (Figure
196 3a, black) fits the data (shaded area: mean $\text{ITD}_{\text{HF}}(\theta)$ over subjects $\pm 1/2$ s.d.), except when
197 the azimuth is in the $70 - 110^\circ$ range, which has been previously documented (Aaronson
198 and Hartmann, 2014). Figure 3B shows the low frequency prediction with Kuhn’s formula
199 (Eq. 3) alongside mean ITD estimated from HRTFs between $f_{\text{norm}} = 0.5$ (290 Hz) and
200 $f_{\text{norm}} = 0.6$ (350 Hz), termed low frequency $\text{ITD}_{\text{LF}}(\theta)$. Consistent with previous reports,
201 the approximation of the low-frequency ITD is reliable.

202 On Figure 3c, the values of ITD across frequency are reported for seven positions on the
203 horizontal plane ($0, 30, 60, 90^\circ$ and the symmetrical positions). Curves represent the average
204 normalized ITD across subjects, and shaded areas are ± 1 s.d.. The standard deviation of
205 the normalized ITDs at each frequency and position was on average $46 \mu\text{s}$ (0.16 normalized).
206 This variability is relatively small: it is about 6% of the maximal ITD value observed, and
207 is about a factor of two larger than a human just-noticeable difference (JND) in ITD (the
208 smallest ITD difference perceptible by human subjects (Mills, 1958)).

209 In addition, the plots on Figure 3c reveal some fine variations of ITD with frequency
210 that are not accounted for by the spherical model (e.g. the low frequency bump for azimuth
211 $\pm 30^\circ$). This reveals that deviations of the human head morphology from a sphere contribute
212 systematically to the ITD versus frequency relationship.

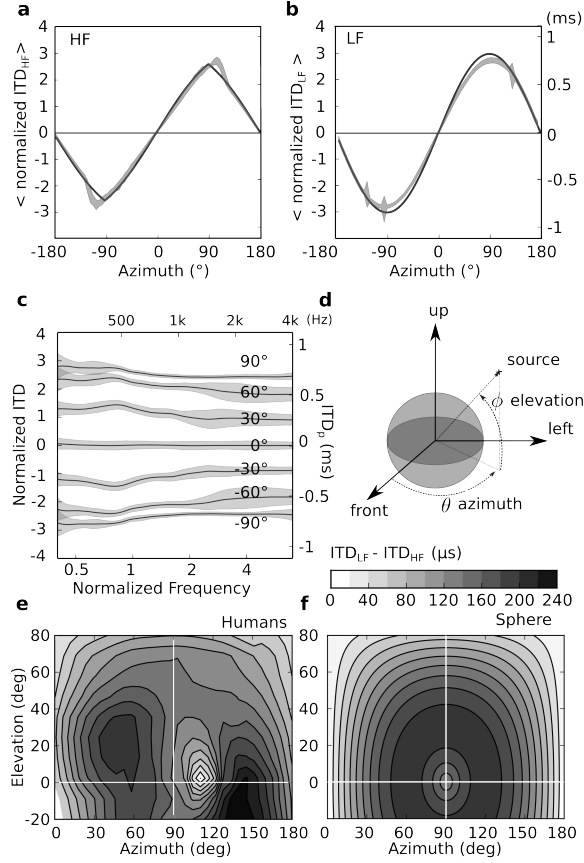


Figure 3: Frequency dependence of ITD in human subjects. (a) Inter-individual average normalized ITD in high frequency as a function of azimuth $\pm 1/2$ s.d. (shaded area). Black line indicates the theoretical value from the Woodworth model (Eq. 2). Corresponding ITD values for a head radius of 9.5 cm are shown on the right of panel b. (b) Average normalized ITD in low frequency $\pm 1/2$ s.d. (shaded area), black line indicates the theoretical value from Kuhn’s formula (Eq. 3). (c) Average normalized ITD (black lines) as a function of frequency for seven source positions (shaded area: $\pm 1/2$ s.d.). (d) Azimuth θ and elevation ϕ are defined in a standard vertical-polar coordinate system (see text). (e) Difference between high- and low-frequency normalized ITD as a function of elevation and azimuth. Physical ITD is calculated for a head radius of 9.5 cm. (f) Same as (e) for the spherical model. Normalized units correspond to a head radius of 9.5cm.

213 3. *Frequency variation of ITD as a function of azimuth and elevation*

214 Consistent with previous reports, our data show that ITD is frequency-dependent in
215 human HRTF, with similar differences between low and high frequency values as in the
216 spherical models in the horizontal plane. We now quantify this difference as a function
217 of both azimuth θ and elevation ϕ . Recall that we used a vertical-polar coordinate system
218 (Fig. 3d). Fig. 3e shows the average difference $\text{ITD}_{\text{LF}} - \text{ITD}_{\text{HF}}$ across subjects for all positions
219 on the spatial grid, converted to physical ITD values assuming head radius of 9.5 cm. For
220 comparison, the same quantity is shown for the sphere on Fig. 3f.

221 The difference between high and low frequency ITD exceeds $50 \mu\text{s}$ for most of the
222 positions on the sphere, and can reach more than $200 \mu\text{s}$. As a comparison, human subjects
223 can discriminate ITDs differing by a JND of only $20 \mu\text{s}$ (Mills, 1958). Therefore, the variation
224 of ITD with frequency should be perceptually significant for most source positions away from
225 the midline.

226 For large enough source distances, the pressure at any point on the surface of a sphere
227 depends only on the angle between the ray from the center of the sphere to the source,
228 and the ray to the measurement point on the surface of the sphere (Duda and Martens,
229 1998). Because of this symmetry property, binaural cues are constant for sources lying on
230 so-called cones of confusion, centered on the interaural axis. In other words, acoustical cues
231 in a spherical head model only depend on the angle of the source acoustical wave and the
232 medial-sagittal plane: the *incidence angle* $\beta = \arcsin(\cos(\phi) \sin(\theta))$. Cones of confusion are
233 then the set of points of equal incidence angle β . This aspect makes it hard to differentiate
234 sound sources positioned symmetric to the interaural axis, which includes front and back
235 positions.

236 Consistent with previous reports in humans, our data show that cones of confusion are
237 centered around source positions directly facing the ears (that is, at the same azimuth and
238 elevation as the ears, Aaronson and Hartmann, 2014). Furthermore, they appear distorted
239 (around $(\theta, \phi) = (110^\circ, 5^\circ)$, Fig. 3e). In particular, the variation of ITD with frequency

240 quantitatively differs between front and back (and up and down) positions.

241 C. Maximal ITD

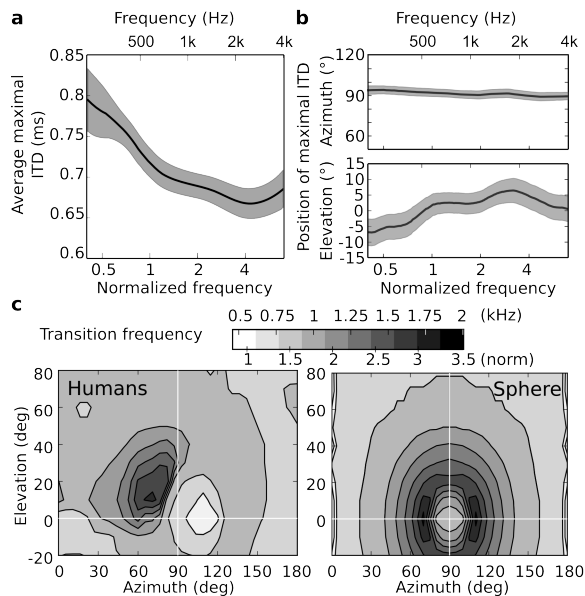


Figure 4: Maximal ITD and transition frequency in human subjects. (a) Maximal ITD across subjects as a function of frequency. (b) Azimuth (top) and elevation (bottom) where ITD is maximal as a function of frequency. Shaded areas of (a) and (b) are the mean $\pm 1/2$ s.d. (c) Transition frequency (see text) as a function of azimuth and elevation in humans (left) and in the spherical model (right). Normalized units converted assuming a head radius of 9.5cm.

242 We estimated, from the *unnormalized* data, the maximal ITD over positions for each
243 frequency and subject (reported here on a normalized frequency scale). By nature, ITD
244 estimation can be unstable in high frequency because of the ambiguity inherent when un-
245 wrapping a phase response, and in low frequency because of the low frequency resolution.
246 This is especially prominent when automatically processing a large number of recordings
247 (several hundred positions, and subjects), and creates many outlier datapoints, which posi-
248 tively biases the estimation of a maximal ITD.

249 The 95% percentile (see, e.g., Papadatos, 1995) is a more robust estimator of sample
250 maximum, which we define here as the maximal ITD. Consistent with the theory and previ-
251 ous reports, we found that the maximal low-frequency ITD value is $813 \mu\text{s} \pm 70 \mu\text{s}$ (s.d., see
252 Fig. 4a). The maximal broadband ITD – computed as the peak lag of the cross-correlated
253 impulse responses, was found to be $612 \mu\text{s} \pm 34 \mu\text{s}$ (s.d.). This value is very close to the
254 value of the maximal high frequency ITD, $688 \mu\text{s} \pm 47 \mu\text{s}$ (s.d., see Fig. 3b).

255 The maximal ITD occurs for azimuth around 95° (Fig. 4b), for which the source is
256 directly facing one of the two ears, which is consistent with previous reports (Aaronson and
257 Hartmann, 2014). There are systematic variations of the position of maximal ITD with
258 frequency, but it remains near eccentric azimuths ($\pm 90^\circ$) and close to the horizontal plane
259 (-10° to 10°). In the spherical model computations, the maximal ITD is reached at $\theta = 90^\circ$
260 (Eq. 3), in humans it occurs for positions slightly more to the back (Fig. 4b), and for
261 sources originating from below or above the horizontal plane, depending on the frequency
262 of the signal (Fig. 4b).

263 D. Transition between ITD regimes

264 It could be argued that even though the ITD varies across frequency, this variation does
265 not occur in the range where ITD is used as a cue to azimuth (i.e. the ITD is constant
266 below 1.8 kHz). To assess this, we examined the shape of the ITD versus frequency curves,
267 specifically trying to get at the frequency at which ITD effectively transitions between its low
268 and high frequency regimes. We define the *transition frequency* as the frequency at which
269 the ITD equals the average between its high frequency ($\text{ITD}_{\text{LF}}(\theta, \phi)$) and low-frequency
270 ($\text{ITD}_{\text{HF}}(\theta, \phi)$) values for a given position. Because in general ITD is a decreasing function of
271 frequency with a relatively narrow transition, this transition frequency allows us to separate
272 frequency regions of high and low ITD values for any position.

273 Figure 4C shows the transition frequency in humans and in the spherical head model
274 (for an infinitely distance source), as a function of azimuth and elevation. The transition

275 frequency increases as the source is moving away from the median sagittal plane, up to an
276 azimuth angle $\simeq 70^\circ$ where a maximum value $f_{\text{tran}} \simeq 2.8$ (3.2 in the spherical model) is
277 reached. It then decreases until a minimum is reached at $\theta \simeq 110^\circ$ and $\phi \simeq 0^\circ$ ($\theta = 90^\circ$ and
278 $\phi = 0^\circ$ in the spherical model).

279 In conclusion, for all positions, transition frequencies are between 1 and 3 (normalized
280 scale), which corresponds to physical frequencies between approximately 600 and 1700 Hz.
281 The ITD thus varies substantially at frequencies within the range where ITD is the dom-
282 inant cue for sound laterality in the horizontal plane (Wightman and Kistler, 1992). The
283 magnitude of transition frequencies in humans is overall similar to the predictions of the
284 spherical model, yet as previously mentioned symmetries seen in the spherical model do not
285 appear in the human HRTF data.

286 IV. ENVELOPE AND FINE-STRUCTURE ITD

287 When a sound wave excites the cochleae, different points on the basillar membranes are
288 preferentially excited by energy in different frequency bands. Many neurons in the auditory
289 system, in particular neurons in the midbrain that are sensitive to ITD, are also tuned
290 to different frequencies and are tonotopically organized. We have shown that ITD varies
291 substantially *across* different frequency bands, that is, between distant auditory filters (Fig.
292 5a). An interesting question is whether ITD also varies substantially *within* a single auditory
293 filter (Fig. 5b), as it would then have direct physiological relevance. We relate this question
294 to the difference between envelope and fine-structure ITD.

295 A. Variation of ITD within a auditory filter

296 We first analyzed the variation of ITD within single channels for each position and
297 subject (same HRTF database as in Section III). The variation of ITD is defined as the
298 difference between the maximum and minimum ITD_p in a frequency band with constant
299 $Q = 4.3$ (one-third octave) or with equivalent-rectangular bandwidths (ERB) (Glasberg

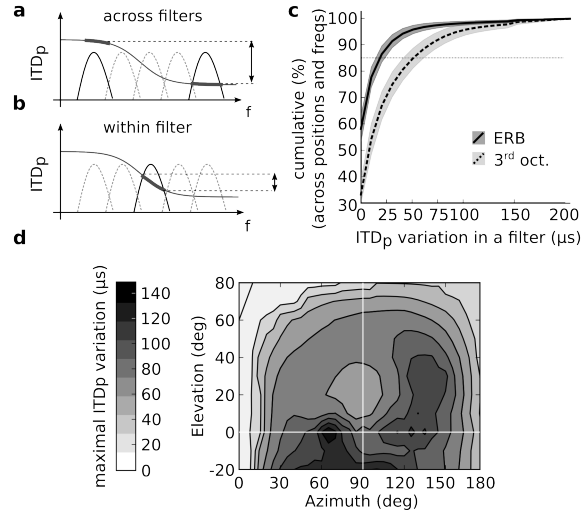


Figure 5: Variation of ITD within single auditory filters. (a) Schematics of the global variation of ITD across different auditory filters. (b) Schematics of the variation of ITD within a single auditory filter. (c) Proportion of positions and center frequencies where ITD variation within a single channel is smaller than a specified value. Lines are averages across population, \pm s.d.. Channel width is either 1 ERB or 1/3 octave. (d) Maximal ITD variation within single channels, as a function of azimuth and elevation, with ERB-wide channels.

300 and Moore, 1990) (Fig. 5b). In the ERB scale, the Q factor value varies between 5 and
 301 9, indicative of the relatively narrow band filtering imposed by the auditory periphery.
 302 We computed the variation of ITD for center frequencies between 350 and 3000 Hz and for
 303 positions close to the horizontal plane ($|\phi| \leq 20^\circ$). We report the cumulative distributions of
 304 ITD variation on Fig. 5c: curves display the percentage of positions and center frequencies
 305 for which the ITD variation is lower than a given amount. In both conditions, for more
 306 than 15 % of the channels and positions the magnitude of the ITD variation is larger than
 307 25 μ s (Fig. 5c). In Fig. 5d, we show the maximal variation of ITD in single channels
 308 as a function of azimuth and elevation (assuming ERB-wide channels). That is, for every
 309 position, we report the variation of ITD in the channel where it varies the most. At specific
 310 source positions, very large variations of ITD can occur within channels (up to 150 μ s): the

311 variation of ITD within a single channel is therefore quite substantial.

The fact that ITD varies within a frequency band means the signal undergoes more than a simple delay when passed through the HRTF. Mathematically, the phase responses of the monaural filters are nonlinear functions of frequency. We can approximate the IPD by an affine (i.e. linear with a non-zero intercept) function of frequency around the center frequency f_0 of a cochlear filter (Fig. 6a):

$$\begin{aligned} \text{IPD}(f) &\stackrel{\text{def}}{=} \text{ITD}_p(f)f \\ &\approx \text{ITD}_g(f_0)(f - f_0) + \text{IDI}(f_0)[1] \end{aligned}$$

312 where phases are expressed in cycle. The slope of this fit is the *group* ITD, which is the ITD
313 of the envelope (Marple Jr, 1999).

314 The intercept IDI is an additional shift in the phase of the fine-structure of the signal
315 (Fig. 6b). This shift only occurs when the phase ITD varies with frequency, i.e., when
316 propagation does not result in a pure delay. For this reason, we termed this binaural cue
317 the *Interaural Diffraction Index* (IDI, see Rebillat *et al.* (2014)). The IDI can be seen as a
318 measure of the difference between group and phase ITDs at any frequency, converted into a
319 phase value: $\text{IDI} = (\text{ITD}_p - \text{ITD}_g)f$. If $\text{IDI} = 0$ cycles, phase and group ITD are equal, and
320 locally frequency-independent. When the IDI is positive, by convention the phase ITD has
321 a higher absolute value than the group ITD, and vice versa when IDI is negative.

322 B. Estimating ITD in the envelope and fine-structure of binaural signals

323 The group ITD is classically defined as the derivative of the unwrapped IPD curve with
324 respect to frequency as represented in Fig. 6a. Because of occasional errors of the phase
325 unwrapping operation, estimating the derivative from large sets of unwrapped IPD curve is
326 unreliable. Instead we use an equivalent approach wherein we perform circular-linear fits on
327 the *wrapped* IPD. The estimation can be formulated as a non linear least square problem,
328 where IDI and ITD_g are chosen to minimize the fit error $\sum_f \|\text{IPD}(f) - (\text{IDI} + \text{ITD}_g f)\|^2$ over
329 a given frequency band, where the norm $\|\cdot\|$ is a norm on phases. Because wrapped phase

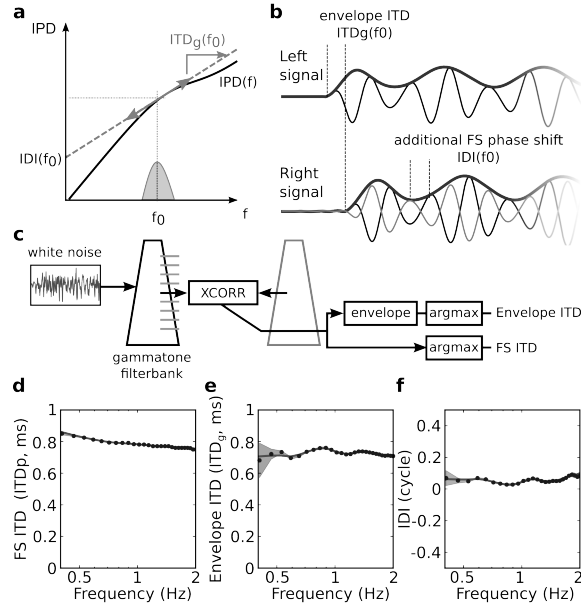


Figure 6: Envelope and fine-structure ITD. (a) The IPD for one position is unwrapped and an affine fit is taken locally around f_0 . The intercept of the fit is the IDI and the slope the group ITD. (b) When the IDI is zero, the delay is frequency-independent and both envelope and fine-structure are delayed by the ITDg (bottom, black signal). When IDI is non zero, the fine-structure undergoes an additional phase shift equal to the IDI (bottom, grey signal). (c) Simulation: white noise is passed through HRTF filters for one position (spherical head model, azimuth = 70°). The resulting signals are then fed into gammatone filterbanks. The responses in the two banks are then cross-correlated, and the result is separated in envelope and fine-structure components. The time lag of the maximum of the cross-correlation is the phase ITD, and that of the maximum of the envelope of the cross-correlation is the envelope ITD (see text). (d) Results of estimating phase ITD, ITD_p , from the IPD (plain line), and from simulations (mean: dots, shaded area: 95% confidence interval). (e) Same as (d) for ITD_g . (f) Same as (d) for IDI.

330 values are a circular quantity, so is the norm we use in the fit. It can be expressed as a cosine
 331 function of its argument: $\|x\|^2 = 1 - \cos(2\pi x)$. The precise algorithm used is described in
 332 more details in the Methods section of Luling *et al.* (2011).

333 To show in practice that group ITD and IDI can be extracted from the envelope and
334 fine-structure of band-limited binaural signals, we simulated a simple model of the auditory
335 periphery. We then computed the envelope and fine-structure ITD in different frequency
336 bands of our auditory model (Fig. 6c) using a standard cross correlation approach. The
337 auditory periphery model consisted of two gammatone filter banks receiving 100-ms-duration
338 white-noise inputs convolved with the spherical HRTFs. Each filter’s response was then
339 cross-correlated with the opposite frequency band. This operation is a good approximation
340 of the response of binaural neurons in the medial superior olive of mammals (Yin and Chan,
341 1990). The fine-structure ITD is obtained by computing the position of the maximum of
342 the cross correlation function. Then, the envelope of the cross-correlation is extracted using
343 a Hilbert transform, and the maximum computed. This procedure yields an estimate of
344 the delay in the envelopes (i.e. it is equivalent to computing the maximum of the cross-
345 correlation of the envelopes Marple Jr (1999)). The results of this simulation are plotted
346 on Fig. 6d-f. Dotted points (with 95% confidence intervals over repeated trials) represent
347 the ITDs estimated using the simplified auditory model. The theoretical predictions (plain
348 lines) were obtained by taking circular-linear fits of the IPD of the HRTF pair used. The
349 match between theory and simulation is excellent, which shows that the group ITD indeed
350 corresponds to the envelope ITD, which appears in the cross-correlation of the monaural
351 signals, and the IDI indeed corresponds to the additional shift of the fine-structure seen in
352 the cross-correlation function.

353 C. Analysis of envelope and fine-structure ITDs in human HRTFs

354 We computed ITDs in the envelope and fine-structure of the human data presented in
355 Section III, according to the methods presented above. On Figure 7 we present the average
356 ITD_p , ITD_g and IDI over the whole population. We observe that ITD_p and ITD_g can be
357 dramatically different in some frequency bands (typically around 1kHz). As a result the IDI
358 is non-zero in that range (Figure 7e), which corresponds to the frequency range just above

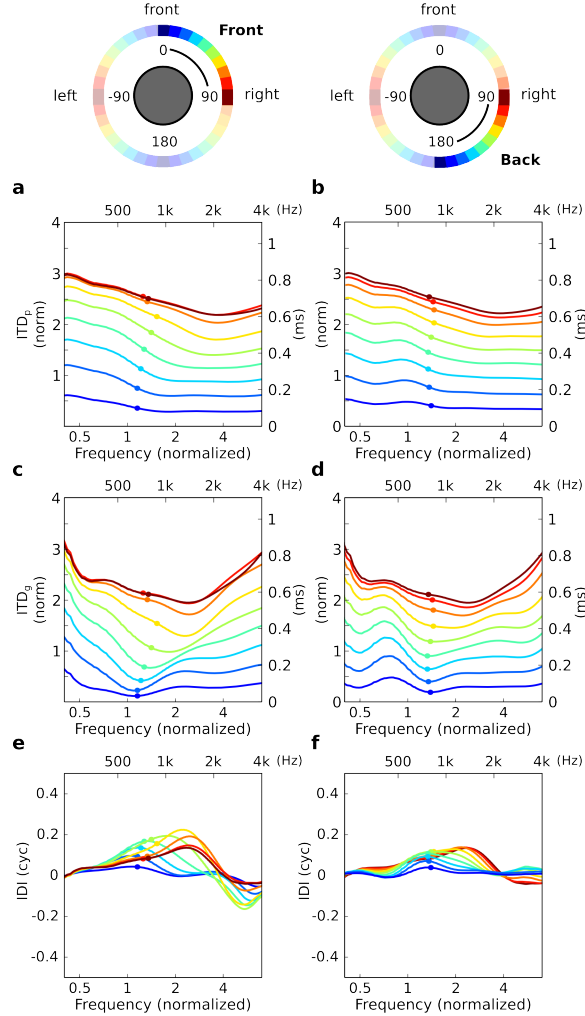


Figure 7: Averages over the whole population of normalized ITD_p (a,b), ITD_g (c,d), and IDI (e,f) for horizontal plane positions as a function of frequency. Top part of the figure depicts the lines color codes (positive azimuths, separated by 10°). Blue lines are more medial positions, and red more eccentric. Left column (a,c,e) displays data from the front positions, right column (b,d,f) from the back positions. Dots overlaid on the line plot represent the position of the transition frequency.

359 the “transition frequency” introduced above (data not shown).

360 For all positions, we find that the IDI is close to zero for lower frequencies. It then
 361 positively increases in low frequencies (below 2-3 kHz) and then drops to negative values for
 362 higher frequencies (above about 4kHz). Therefore, generally the fine-structure ITD is higher

363 than the envelope ITD for frequencies between 1 and 3 kHz, and smaller in high frequencies
364 (around 4kHz). While both ITDs are monotonically increasing functions of eccentricity
365 (Figure 7a-b, c-d), the relationship is more complex for IDI. In addition, as noted in the
366 above statistical analyses, the frequency-dependence of ITD is different for front and back
367 positions (Figure 7e,f), which is potentially a cue to disambiguate between them.

368 V. FREQUENCY-DEPENDENCE OF ITD IN ANIMALS

369 In many animal species, neurons tuned to ITD have been identified, e.g. in the Medial
370 Superior Olive (MSO) or Inferior Colliculus (IC) of mammals (Yin and Chan, 1990). A
371 recent debate has emphasized the importance of the natural distribution of binaural cues in
372 our understanding of electrophysiological data (Grothe *et al.*, 2010). In this context, and
373 more generally in neurophysiological studies of sound localization, binaural cues (ITD and
374 Interaural Intensity Differences, IID) have been measured for a number of animal species,
375 including mammals, but also birds and reptiles.

376 As seen in humans, a strong dependence on morphological features of the animals is
377 found in many instances. For example, the owl’s facial ruff (Campenhausen and Wagner,
378 2006), or the cat’s pinnae (Tollin and Koka, 2009) increase the magnitude of ITD at a given
379 position. However, the variation of ITD with frequency has received little attention until
380 recently (Benichoux *et al.*, 2015). We applied the same analysis as above to measured HRTFs
381 of different animal species.

382 A. Animal HRTF recordings

383 We measured the HRTFs of six taxidermist animal models, using the same setup as
384 for the human recordings (LISTEN-V2, see Table I): rat, rabbit, guinea pig, chinchilla,
385 cat and macaque. All animals had their ear canals obstructed by the taxidermy, which
386 means that recordings are taken in a blocked-meatus configuration. Animal models were
387 chosen according to the well-preserved quality of their pinnae. We previously showed that

388 HRTFs measured on taxidermist models agree closely with acoustical simulations based on
389 3D models of the animal with rigid boundaries (Rebillat *et al.*, 2014).

390 In general, animal models were in a natural-looking position, in which the head of the
391 animal is not aligned with the body. Therefore, the coordinate system is rotated so that
392 the head points in the 0° direction. This is achieved by computing the *head angle* relative
393 to the body: the azimuth that minimizes the magnitude of the low-frequency ITD value.
394 Head angles were generally non-zero for all models (rat 10° , rabbit -10° , guinea pig 20° ,
395 chinchilla -20° , cat -55° , macaque -30°). It should also be noted that the interaural distance
396 of the rabbit, guinea pig and macaque models in the present study are noticeably smaller
397 than those of animals of the same species whose recordings are reported in the literature
398 (see Table II).

399 B. Frequency-dependent ITD in animals

400 A difference between low- and high-frequency ITD in animals has been previously shown
401 in a number of animal species: in the rat (Koka *et al.*, 2008), rabbit (Kim *et al.*, 2010), guinea
402 pig (Greene *et al.*, 2014), chinchilla (Lupo *et al.*, 2011; Koka *et al.*, 2011), cat (Roth *et al.*,
403 1980; Tollin and Koka, 2009) and macaque monkey (Spezio *et al.*, 2000). Yet, only very
404 few studies reported the frequency-dependent ITD curves for many azimuth positions. The
405 phase ITD for all animal models and frequencies between 350 and 3000 Hz is reported on
406 Fig. 8, for positions in the horizontal plane. Consistent with physical acoustics, and the
407 above results in humans, the phase ITD is frequency-dependent in all species.

408 Because humans are bipeds, no part of the body normally finds itself on the way between
409 the source and the ears. In many quadrupeds, for example in the cat (Fig. 8e), sounds
410 coming from the back can be reflected or scattered by the body before reaching the head
411 and ears. This morphological asymmetry results in large differences between the frequency-
412 dependent ITDs of sources in the front (solid curves) and in the back (dashed). Thus in
413 principle, front and back positions can be distinguished on the basis of the ITD at different

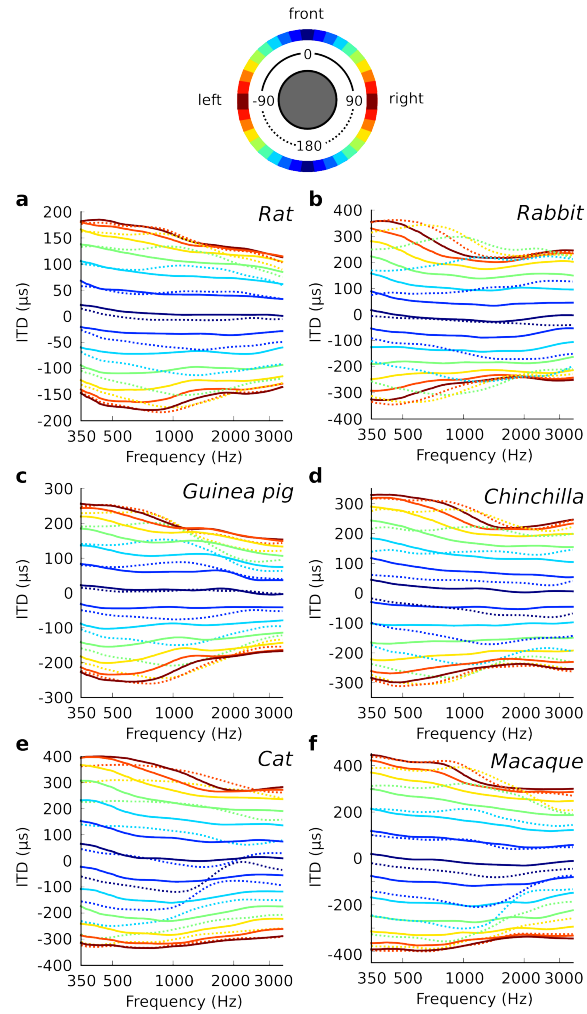


Figure 8: Animal ITDs in the horizontal plane, for 24 positions around the head (separated by 15°). Top: line color code; front positions, solid lines; back, dashed lines. (a) Rabbit, (b) Guinea pig, (c) Chinchilla, (d) Cat, (e) Rat, (f) Macaque.

414 frequencies. Similarly, it was shown using acoustical measures and simulations that the
 415 posture of the animal influences the frequency-dependent pattern of ITD (Rebillat *et al.*,
 416 2014).

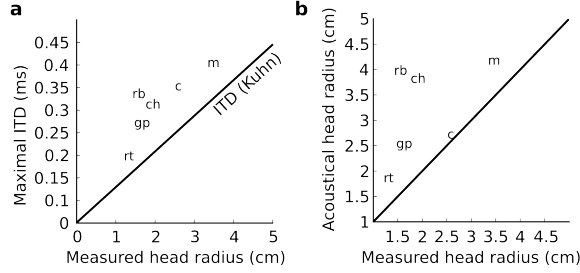


Figure 9: Comparison of measured ITD range with anatomy. (a) Maximal measured low-frequency ITD as a function of half the interaural distance measured on the taxidermist models. Predictions are shown for Kuhn’s formula (solid). (b) Acoustical head radius estimated with Woodworth’s formula (see Text) vs. half the interaural distance measured on the taxidermist models (dashed line: diagonal). Legend: rb: rabbit; ch: chinchilla; gp: guinea pig; m: macaque; rt: rat; c: cat.

417 C. Estimating animal ITD from head size

418 For electrophysiological studies, a way to estimate the maximal ITD for a given animal
 419 species is to measure the interaural distance and then use one of Woodworth’s (Eq. 2) or
 420 Kuhn’s formula (Eq. 3). The maximal ITD is thus obtained in low frequencies (via Eq. 3)
 421 for the most eccentric position, that is $ITD_{\max} = 3a/c$. However, in some species there is
 422 evidence that this method yields an underestimation of the maximal ITD (see, e.g. (Tollin
 423 and Koka, 2009) in the cat). “ In Fig. 9a, the maximal ITD measured in the horizontal
 424 plane is reported as a function of the half interaural distance of the animal, measured as the
 425 half distance between the entrances of the (occluded) ear canals. In all cases, the maximal
 426 ITD is well correlated with the physical head size, but substantially larger than predicted
 427 using the Kuhn formula. We further computed the *acoustical head radius* for each animal
 428 model, as we did in humans (see Section III). Consistent with previous observations (e.g.
 429 (Tollin and Koka, 2009)), the *acoustical* head radius of animals is substantially larger than
 430 their physical “head radius” (the half interaural distance of the animal model, Fig. 9b).

431 Overall, our animal results suggest that the maximal ITD should not be estimated from

432 a crude measure of the morphology of the animal (here interaural distance), because this
433 leads to a systematic underestimation of the magnitude of ITD for all species.

434 VI. SUMMARY AND DISCUSSION

435 A. Summary

436 In this paper, we have quantified the variation of ITD with frequency in humans and
437 animals, measured in anechoic space. First, we confirmed that ITD does vary significantly
438 with frequency, as predicted by a spherical head model (Kuhn, 1977) and mentioned in
439 previous studies (Wightman and Kistler, 1989). Specifically, maximal ITD values were
440 found to be about 800 μs in low frequencies and 600 μs in high frequencies. Therefore, the
441 low frequency ITD can be larger than the high frequency ITD by as much as 200 μs , which
442 is an order of magnitude larger than human JNDs in ITD discrimination tasks (of the order
443 of 20 μs), even for pure tones (Brughera *et al.*, 2013) (10-40 μs for frequencies below 1250
444 Hz). The transition between low- and high-frequency ITDs occurs at frequencies between
445 600 and 1800 Hz, within the range where ITD is a dominant cue for localization in the
446 horizontal plane (Wightman and Kistler, 1992).

447 Additionally, we observe that the frequency-dependence of ITD does not exhibit sim-
448 ple spherical symmetries. In particular, symmetrical front and back (and up and down)
449 positions, both in humans and animals, have different frequency-dependent ITDs. The fre-
450 quency dependence of ITD provides, in addition to azimuth, a cue to elevation including
451 information about front versus back.

452 We also show that for multiple of source positions, ITD varies not only globally across
453 the spectrum, but also locally within the bandwidth of a single auditory filter. This causes
454 different ITDs for envelope and fine-structure, which can provide additional information
455 about the position of the sound source. Furthermore, those cues can be estimated from
456 binaural signal using cross-correlation. The difference in group and fine-structure ITD is
457 quantified by the *interaural diffraction index* (IDI).

458 B. Relation with psychoacoustical experiments

459 A few studies have examined the sensitivity of human subjects to the frequency-
460 dependence of ITD. Kistler and Wightman (1992) showed that localization errors for bursts
461 of white noise are similar with individual HRTFs compared to HRTFs in which the monaural
462 phase information was degraded. However, these manipulated HRTFs — minimum-phase
463 filters, do in fact preserve the frequency-dependence ITDs, in a way known to be close to
464 those of measured HRTFs (Kulkarni *et al.*, 1999).

465 In a study on the cues for externalization of sounds, Hartmann and Wittenberg (1996)
466 showed that human subjects are unable to detect the substitution of the phase information
467 of HRTFs by a properly adjusted frequency-independent ITD. The test was done for a source
468 location at 37° on the horizontal plane, in an anechoic room. According to our analysis, at
469 that location the ITD varies by about $130 \mu\text{s}$ across frequency and the transition frequency
470 is 900 Hz (about 1.6 in normalized frequency). Kulkarni *et al.* (1999) also found that human
471 subjects were unable to discriminate individual HRTFs from linear phase HRTFs, as long as
472 the average low-frequency ITD was correct. Constan and Hartmann (2003) also showed that
473 subjects cannot determinate whether binaural sounds have frequency-independent ITDs or
474 frequency-dependent ITDs as in the spherical model — however, neither of these two cases
475 is entirely realistic.

476 The fact that human subjects cannot perceive the difference is puzzling, because they
477 can detect ITD changes of $10\text{-}40 \mu\text{s}$ in pure tones below 1250 Hz (Brughera *et al.*, 2013).
478 Furthermore, in a two-dimensional absolute localization task the mean error is about 5° in
479 the frontal hemifield (for broadband noise bursts, Makous and Middlebrooks (1990)), which
480 corresponds to about $50 \mu\text{s}$ ITD. As the ITD variation across the spectrum can reach 200
481 μs for some positions, systematic frequency-dependent errors should be observed if the ITD
482 variation were discarded.

483 Together, these studies suggest that human subjects can detect small ITD changes in
484 tones when they are presented in isolation, but they cannot detect them when they are

485 embedded in a complex sound, as long the average ITD is unchanged. This is consistent
486 with the notion that source location is inferred from the pattern of ITD, but that only that
487 inferred location, rather than the acoustical cues, is available to conscious perception and
488 behavior, and in particular is used in discrimination tasks. Thus, two sounds with different
489 patterns of frequency-dependent ITD are indistinguishable if they yield the same estimated
490 location. This is consistent with other aspects of binaural hearing. In particular, it has been
491 shown that the sensitivity to interaural intensity differences (IID) is substantially degraded
492 when the use of intracranial position as a cue is eliminated by roving the the ITD of the
493 stimuli (Bernstein, 2004).

494 A possible experiment to determine whether ITD information is discarded in estimating
495 the location of the source is to include judgements of the position of sounds with different
496 frequency contents. For example, localization performance could be tested as in measured
497 HRTFs with linear phase HRTFs, but with band-pass filtered noises in different frequency
498 regions. If the frequency-dependence of ITD is discarded, then results should be identical
499 in the two conditions (provided the ITD of linear phase HRTFs is adjusted). On the other
500 hand, if the variation of ITD is indeed taken into account to estimate source position, we
501 should observe systematic errors depending on frequency and position.

502 C. Binaural coherence

503 Binaural coherence is defined as the maximal value of the cross-correlation of monaural
504 signals (Gabriel and Colburn, 1981). Humans are very sensitive to small changes in bin-
505 aural coherence, usually modeled by adding a small amount of independent noise at each
506 ear (usually below 3-4% for noise (Gabriel and Colburn, 1981)). In HRTF recordings, bin-
507 aural coherence is found to be mainly affected by the amount reverberation in the room:
508 binaural coherence is very high in anechoic environments, and dramatically goes down as
509 the environment gets more reverberant (Hartmann *et al.*, 2005). It can be argued that the
510 effect of the variation of ITD within an auditory filter is a decreased coherence (Constan

511 and Hartmann, 2003). Yet, in anechoic conditions this effect remains marginal, especially
512 for the narrow bands of noise resulting from filtering by the auditory periphery (less than
513 0.1% (Constan and Hartmann, 2003)).

514 We argue here for a different interpretation of the frequency-dependence of ITD. De-
515 coherence due to reverberation is intrinsically non-deterministic: different wavefronts reach
516 the listener at different times depending on the unknown geometry of the room. On the
517 other hand, we have shown above that the frequency-dependence of ITD has a fully deter-
518 ministic effect: envelope and fine-structure ITD cues are affected in a way that is predicted
519 by the morphology of the subject. Decoherence, insofar as it is non-deterministic, objec-
520 tively makes the task of recovering the ITD from the cross-correlation function harder. It
521 is unclear, however, why imposing different ITDs in the envelope and fine structure of the
522 monaural signals would make the recovering of ITDs harder, because it is fully deterministic.
523 Therefore, we argue that the variation of ITD in small frequency bands is best thought of as
524 imposing different ITDs in the envelope and fine-structure of monaural inputs, rather than
525 as causing binaural decoherence, as imposed by adding independent white noise to monaural
526 inputs.

527 **D. Signal processing of binaural sounds**

528 Our results are relevant to two classes of signal processing applications: reproduction
529 of binaural sounds and sound localization algorithms. The large variation of ITD with
530 frequency suggests that it is important for proper reproduction of binaural sounds. However,
531 it could be that humans can adapt to non-natural ITD patterns, as they do to spectral cues
532 (Wanrooij and Opstal, 2005). In either case, we note that replacing frequency-dependent
533 ITDs with fixed ITDs removes some potential cues to elevation.

534 State-of-the-art sound localization algorithms using HRTF-filtered inputs do use the
535 frequency-dependence of ITD to estimate source location. In the algorithm described by
536 May *et al.* (2011), sounds are divided into frequency bands, and position is estimated with a

537 maximum likelihood approach from the overall ITDs in these bands. Because ITD likelihood
538 for each position is measured with KEMAR HRTFs, this algorithm uses the variation of ITD
539 across channels. However, it does not use the variation of ITD within channels.

540 Other algorithms use HRTF data with the within-channel ITD variations preserved,
541 (Durkovic *et al.*, 2011; Macdonald, 2008) and were shown to perform well in realistic condi-
542 tions. In each frequency band, monaural signals are convolved with the contralateral HRTF
543 of a candidate source position (i.e., left signal with right HRTF), and the position giving the
544 highest cross-correlation is picked. A spiking neural model relying on similar ideas was also
545 previously presented (Goodman and Brette, 2010): it used cross-correlation, biophysically
546 modeled with coincidence detection between spike trains, and performed better when the
547 variation of ITD within channel was taken into account.

548 E. Electrophysiology

549 The firing rates of neurons in several auditory brainstem nuclei, in particular the me-
550 dial superior olive (MSO) and inferior colliculus (IC) of mammals, is sensitive to the ITD
551 of binaural sounds (Grothe *et al.*, 2010). Similar to humans, we have shown that ITD is
552 frequency-dependent in animals, in the frequency range where it is used for sound localiza-
553 tion (Fig. 8). Furthermore, we showed that asymmetries in this frequency-dependence exist
554 between front and back positions, presumably due to reflections on the back of the animals
555 (Fig. 8). Finally, we have noted that the maximal ITD is generally larger than when esti-
556 mated from simple morphological considerations (Fig. 9). All these observations should be
557 taken into account when interpreting electrophysiological measurements.

558 In the physiological literature, two types of frequency-dependent properties have been
559 discussed (Grothe *et al.*, 2010; Day and Semple, 2011; Benichoux *et al.*, 2015). The preferred
560 ITD of binaural neurons, i.e., the ITD that elicits the largest firing rate, depends on their
561 preferred frequency: at the level of the population those quantities are inversely correlated.
562 This observation has been seen as a challenge to the mainstream theory, according to which

563 neurons are tuned to the ITD of particular source locations, which should cover all possible
564 locations independently of the frequency band (Grothe *et al.*, 2010). In our animal mea-
565 surements, ITD is also larger in lower frequencies than in high frequencies — although to a
566 smaller extent than in electrophysiological recordings. An additional contribution to large
567 low-frequency ITDs in animals is early reflections on the ground, which produce arbitrarily
568 large ITDs in low frequencies (Gourevitch and Brette, 2012).

569 Many binaural neurons also display a second type of frequency-dependence: for a given
570 neuron, the preferred ITD depends on the frequency of the sound (Day and Semple, 2011).
571 We have shown that ITD varies also with frequency within an auditory filter, which provides
572 a potential ecological explanation of this variation (Benichoux *et al.*, 2015). The present
573 analysis suggests that cells with frequency-dependent best delays should be differentially
574 sensitive to envelope and fine-structure delays.

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| Database | N_s | $\Delta\theta$ | $\Delta\phi$ | N_{sub} | Room type |
|-----------|-------|-------------------|-------------------|-----------|---------------|
| LISTEN-V1 | 8192 | 15° | $\simeq 15^\circ$ | 49 | Anechoic |
| LISTEN-V2 | 8192 | 5° | $\simeq 15^\circ$ | 35 | Anechoic |
| CIPIC | 200 | $\simeq 10^\circ$ | 5.6° | 36 | Anechoic |
| ARI | 2400 | 5° | 10° | 10 | Semi-anechoic |

Table I: Overview of the different human HRTF databases used in this study. For each database, the sampling frequency is 44.1 kHz. N_s : length of the head-related impulse responses in samples. $\Delta\theta, \Delta\phi$: approximate spatial resolution in azimuth and elevation. N_{sub} : number of subjects from each database included in the present study. The LISTEN database consists of the 49 subjects freely available on the IRCAM website (LISTEN-V1) and of 35 subjects measured later with an increased spatial resolution in azimuth (LISTEN-V2). Measurements for the ARI database have been performed under semi-anechoic conditions and because of measurement artifacts, only 10 subjects have been retained and the spatial resolution in elevation has been decreased to 10° .

| Animal | Max ITD | | Interaural distance | | |
|------------|-------------|-------------|---------------------|----------------------|------------|
| | LF | HF | Tax. models | Reported | Acoustical |
| Rat | 165 μ s | 134 μ s | 2.7 cm | 2.96 cm ¹ | 3.78 cm |
| Rabbit | 319 μ s | 246 μ s | 3.2 cm | 5.6 cm ² | 8.02 cm |
| Guinea pig | 242 μ s | 184 μ s | 3.35 cm | 4.94 cm ³ | 5.02 cm |
| Chinchilla | 293 μ s | 240 μ s | 3.9 cm | 3.6 cm ⁴ | 7.68 cm |
| Cat | 335 μ s | 276 μ s | 5.2 cm | 5.6 cm ⁵ | 5.44 cm |
| Macaque | 393 μ s | 310 μ s | 7.0 cm | 10.4 cm ⁶ | 8.36 cm |

Table II: Overview of the animal ITD data. Maximal ITDs measured in low and high frequencies for the animal HRTFs. Interaural distances are the distances measured between the ear canal entrances of the taxidermized models (Tax. models), or the value as reported in previous studies (Reported), or twice the acoustical head radius (Acoustical, estimated from ITDs). References: ¹(Koka *et al.*, 2008), ²(Kim *et al.*, 2010), ³(Greene *et al.*, 2014), ⁴(Lupo *et al.*, 2011), ⁵(Roth *et al.*, 1980), ⁶(Spezio *et al.*, 2000) .

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