Human cortical responses to slow and fast binaural beats reveal multiple mechanisms of binaural hearing

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Ross B, Miyazaki T, Thompson J, Jamali S, Fujioka T. Human cortical responses to slow and fast binaural beats reveal multiple mechanisms of binaural hearing. J Neurophysiol 112: 1871–1884, 2014. First published July 9, 2014; doi:10.1152/jn.00224.2014.—When two tones with slightly different frequencies are presented to both ears, they interact in the central auditory system and induce the sensation of a beating sound. At low difference frequencies, we perceive a single sound, which is moving across the head between the left and right ears. The percept changes to loudness fluctuation, roughness, and pitch with increasing beat rate. To examine the neural representations underlying these different perceptions, we recorded neuromagnetic cortical responses while participants listened to binaural beats at a continuously varying rate between 3 Hz and 60 Hz. Binaural beat responses were analyzed as neuromagnetic oscillations following the trajectory of the stimulus rate. Responses were largest in the 40-Hz gamma range and at low frequencies. Binaural beat responses at 3 Hz showed opposite polarity in the left and right auditory cortices. We suggest that this difference in polarity reflects the opponent neural population code for representing sound location. Binaural beats at any rate induced gamma oscillations. However, the responses were largest at 40-Hz stimulation. We propose that the neuromagnetic gamma oscillations reflect postsynaptic modulation that allows for precise timing of cortical neural firing. Systematic phase differences between bilateral responses suggest that separate sound representations of a sound object exist in the left and right auditory cortices. We conclude that binaural processing at the cortical level occurs with the same temporal acuity as monaural processing whereas the identification of sound location requires further interpretation and is limited by the rate of object representations.

Binaural beat; binaural hearing; sound localization; opponent-channel code; hemispheric asymmetry; gamma oscillation; steady-state responses; phase synchrony; magnetoencephalography; auditory cortex

BINAURAL HEARING based on interaural time differences (ITDs) is important for multiple perceptual abilities such as localizing sound in the horizontal plane (Wightman and Kistler 1992) as well as improving speech understanding in noise through segregating sound sources in space (Hawley et al. 2004). Both perceptual qualities show noticeable different temporal dynamics. Perception of sound motion is limited in speed by a time constant of several hundred milliseconds or ~3 Hz for periodic movements (Grantham and Wightman 1978). In contrast, binaural temporal modulation, important for speech understanding, is perceived with high temporal acuity, similar to the sensitivity for monaural temporal modulation (Siveke et al. 2008). This suggests that multiple levels of temporal processing of binaural cues exist at the cortical level.

While birds use multiple channels of ITD detection and establish a topographic map of sound locations at the level of the auditory brain stem (Carr and Konishi 1990; Konishi 2003), mammals use only a single channel of coincidence detection for each hemisphere and encode the sound location through asymmetry of activation in broadly tuned bilateral channels (Grothe et al. 2010). This opponent-channel model was supported by the finding of spatially selective neurons in the inferior colliculus (McAlpine et al. 2001) and the auditory cortex (Stecker et al. 2005). How this encoding of binaural cues is interpreted at the cortical level is still an open research question. Besides generally larger cortical responses contralateral to the sound location, it seems unlikely that a spatial map is solely based on hemispheric imbalance. For example, that the right hemispheric is dominantly involved in sound localization has been concluded from findings that spatial neglect patients with right hemispheric lesions are often unable to localize sound (Zimmer et al. 2003). However, spatial hearing is commonly preserved if a unilateral lesion is confined to the auditory cortex, suggesting that spatial maps exist in bilateral auditory cortices (Zatorre and Penhune 2001). Similar findings of spared sound lateralization have been reported in patients with auditory cortex lesions, in contrast to more general deficits in dichotic listening, which were found in patients with extensive unilateral lesions. A recent TMS study demonstrated parallel processing of sound identity features in anterior auditory cortex and sound location in posterior auditory cortex (Ahveninen et al. 2013).

Thus it seems that opponent-channel coding of sound is already established at the level of the inferior colliculus, and the auditory cortex may have the role of an overarching interpreter for perception. Observing how auditory cortices respond to spatial hearing may inform about underlying neural mechanisms at and below the auditory cortex. Several recent studies of auditory cortex responses provided direct evidence for the opponent-channel model using stimuli that specifically manipulated ITD (Magezi and Krumbholz 2010), recording auditory evoked potentials in sound field stimulation (Briley et al. 2013), and using a stimulus adaptation paradigm in MEG (Salminen et al. 2009). Thus our aim was to expand on the previous research and use binaural beats and acoustic beat stimuli to study the cortical processes of ITD across a wide range of frequencies.
EEG and MEG are the methods of choice for examining time-sensitive cortical processes in humans because of their high temporal resolution. Previous EEG and MEG studies on cortical responses to ITD processing reported either transient responses to sudden changes in the interaural time or phase relation (Chait et al. 2005, 2007; Jones et al. 1991; McEvoy et al. 1990; Ross et al. 2007a, 2007b; Schröger and Wolff 1996; Soeta et al. 2004) or steady-state responses evoked with periodic stimulation (Dajani and Picton 2006) and directly with binaural beating (Draganova et al. 2008; Karino et al. 2006; Schwarz and Taylor 2005) to address the temporal dynamics of binaural hearing. However, these studies have never addressed systematically how frequency-dependent processes of binaural hearing are differently represented in human auditory cortex.

In this study, we used the binaural beat paradigm for studying binaural processing at slow and fast rates. Dichotic presentation of two pure tones with slightly different frequencies $f_1$ and $f_2$ induces a rhythmic sensation at the difference frequency $\Delta f = f_2 - f_1$, which is termed the binaural beat (Stewart 1917). Perception of the binaural beat requires neural interaction. In contrast, the physical superimposition of the same tones results in a beating sound, synonymously termed the physical beat, acoustic beat, or monaural beat. Therefore, sometimes the distinction is made between the “central” (binaural) beat and the “peripheral” (acoustic) beat. Psychoacoustical studies have shown that the perceptual quality of the binaural beat depends primarily on the frequency region of the tones and on the frequency difference between the tones (Licklider et al. 1950; Perrott and Nelson 1969). At $f_1, f_2 \approx 500$ Hz, where the binaural effects are strongest, we can distinguish between four types of perception, depending on the beat rate. At $\Delta f$ below $\sim$3 Hz, the binaural beat is perceived as rhythmic change in the lateralization of the sound, sometimes termed a rotating tone (Perrott and Musicanit 1977). As $\Delta f$ increases, the percept of motion changes to fluctuation of loudness and becomes a rough sound above $20–25$ Hz. At higher $\Delta f$, finally, two separate tones are perceived with different pitches in each ear (Licklider et al. 1950). The transitions between the various percepts are not sharply defined. The various binaural beat percepts primarily correspond to different qualitative perceptions of amplitude-modulated (AM) sound or the acoustic beat, which also depend on the modulation frequency or $\Delta f$, respectively. Below $\sim$3 Hz, distinct sound bursts are perceived as single auditory events. The AM bursts fuse into a sound stream with fluctuating amplitude when the modulation frequency increases. A rough buzzing sound is perceived above $\sim$25 Hz, and at higher AM frequencies the spectral components are resolved and perceived as distinct pitches. More recent studies have shown that binaural beat perception is not limited to tonal stimuli and can be created by binaural noise stimuli, in which spectral phase and amplitude components are transposed slightly in one ear relative to the other (Akeroyd 2010; Dietz et al. 2008; Siveke et al. 2008). Interestingly, the salience of sound motion at low frequencies may be even more pronounced for noise than for pure tones.

When using the binaural beat stimulus, it is important to separate characteristics of the cortical responses that reflect the general processing of rhythmic sound and those that reflect specific properties of binaural hearing. For this reason, several previous studies compared cortical responses to binaural and monaural beats (Draganova et al. 2008; Pratt et al. 2009, 2010).

One limitation of those studies was that only a single beat rate or a small number of beat rates was investigated. Consequently, it is unknown whether the results found at different frequencies in those studies, especially about hemispheric asymmetries of response amplitudes and phases, were caused by different experimental approaches or truly reflect the coding schemata for both the monaural and the binaural beats across the range of beat rates. Therefore our main experimental approach was to compare brain responses to the acoustic beat and the binaural beat elicited by two-tone complexes while continuously sweeping the beat frequency between 3 Hz and 60 Hz.

When comparing brain responses to both binaural and acoustic beating, one should consider the different saliences of the two types of beat sensation. The perceptual strength of the binaural beat is relatively weak compared with a same-intensity monaural two-tone complex. For matching the sensation strength of a binaural beat with the loudness fluctuation of an AM sound, the modulation index $m$ was varied in several studies. In the 500-Hz range and at beat rates between 3 Hz and 4 Hz, a matching AM depth of $m = -25$ dB was found at stimulus intensities between 30 dBSSL and 60 dBSSL (Groen 1964; Grose et al. 2012; Rutschmann and Rubinstein 1965). This means that about $\pm 5\%$ amplitude fluctuation in the AM sound is sufficient to produce a sensation strength equivalent to that of the binaural beat.

For our experimental design, we had to choose whether to match the sensation strength of an AM sound for the acoustic beat stimulation, which would allow a fair quantitative comparison of binaural beat and acoustic beat responses. Alternatively, we chose to use same-intensity two-tone complexes, which resulted in noticeably larger responses for the acoustic beat. At first, this allowed us to study the temporal dynamics of the cortical responses evoked by the acoustic beat across a wide frequency range, the results of which have been reported recently (Miyazaki et al. 2013). In the present study, we analyzed the binaural beat responses in the frequency domain, which improved the signal-to-noise ratio through integration over time. This approach allowed a detailed comparison of the binaural beat responses and acoustic beat responses across beat rates between 3 Hz and 60 Hz.

MATERIALS AND METHODS

Participants. Fifteen healthy adults (7 women, 8 men) aged 19–40 yr (mean 24.4 yr) participated in this study. Hearing thresholds between 250 Hz and 8,000 Hz were below 20-dB normal hearing as tested in a soundproof audiometric booth with a clinical audiometer (GSI 61, Grason-Stadler, Eden Prairie, MN) and according to the guidelines of the American Speech-Language-Hearing Association (1978). According to self-reports, three participants were left-handed and the others were right-handed. None of the participants reported a history of otological or neurological disorders. All provided their consent in written form after being informed about the nature and aim of the study in accordance with protocols reviewed and approved by the Research Ethics Board at Baycrest Centre. Participants received an honorarium.

Stimuli and procedure. Two pure-tone stimuli with frequencies $f_1 < f_2$ presented dichotically induced the binaural beat. Dicotic presentation of the sum of both tones generated the acoustic beat. The interaction between the two tones results in an amplitude fluctuation in case of the acoustic beat (see Fig. 9B) and fluctuations of the interaural phase difference (IPD) for the binaural beat (see Fig. 9C).

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We varied the difference frequency $\Delta f$ smoothly from 3 Hz to 60 Hz and back over a 16-s time interval, while keeping the mean of $f_1$ and $f_2$ equal to 500 Hz. We designed the time course of $\Delta f$ such that the frequency gradient linearly increased between 0 and 15 Hz/s. In the binaural beat condition, we presented the lower-frequency tone $f_1$ (498.5–470 Hz) always to the right ear and the higher-frequency tone $f_2$ (501.5–530 Hz) to the left ear. The stimulus intensity was 65 dB above the individual sensation threshold for a single 500-Hz tone, which was assessed at the beginning of each session. Stimuli were presented with ER3A transducers (Etymotic Research, Elk Grove Village, IL), which were connected to the participant’s ears via 3.4-m-long plastic tubes and foam earplugs. We considered the acoustic transmission delay of 10 ms during data analysis. The stimulation was controlled by Presentation software (Neurobehavioral Systems, Albany, CA).

**Behavioral test.** We presented two-tone complex sounds of 1-s duration with $\Delta f$ between 0 Hz and 60 Hz in 5-Hz steps in random order as acoustic or binaural beat stimuli. The mean frequency of the two tones was always 500 Hz. The participants judged for each stimulus whether the sound was steady or beating.

**MEG recording.** The MEG was recorded in a quiet magnetically shielded room with a 151-channel whole-head axial gradiometer-type MEG system (VSM Medtech, Port Coquitlam, BC, Canada) at the Rotman Research Institute. Participants were seated comfortably in an upright position with the head resting inside the helmet-shaped MEG sensor. They watched a closed-captioned silent movie of their choice to maintain a constant level of vigilance. The head location relative to MEG sensors was registered at the beginning and end of each recording block with electromagnetic coils attached to the nasion and left and right preauricular points. The mean of repeated fiducial locations defined the head-based Cartesian coordinate system with the origin at the midpoint between the bilateral preauricular points. The postero-anterior $x$-axis was oriented from the origin to the nasion, the mediolateral $y$-axis (positive toward the left ear) was perpendicular to $x$ in the plane of the three fiducials, and the inferior-superior $z$-axis was perpendicular to the $x$–$y$ plane (positive toward the vertex). The MEG was recorded in blocks of 390-s duration (6.5 min), containing 24 sweep periods each. Five blocks with acoustic beat stimulation and eight blocks with binaural beat stimulation were repeated in random order in two MEG sessions of $<1$-h duration each. The larger number of recording blocks for the binaural beat was chosen because previous studies showed significantly smaller responses compared with the acoustic beat. A block was repeated when the fiducial locations differed more than $\pm 5$ mm from the mean. Most participants performed both sessions on the same day; otherwise, participants came on the following day.

**MEG data processing and source estimation.** The magnetic field data were low-pass filtered at 200 Hz, sampled at 625 Hz, and stored continuously. From the continuous data, the time points of eyeblink and heartbeat artifacts were identified with independent component analysis (Illie et al. 2002). The MEG was averaged according to eyeblink and heartbeat events, respectively, and the first principal components of the averaged artifacts were used as spatiotemporal templates to eliminate artifacts in the continuous data (Kobayashi and Kuriki 1999).

Dipole source analysis was performed based on the 40-Hz responses evoked by the acoustic beat, which was the most prominent response component (Miyazaki et al. 2013). Short 200-ms intervals of the MEG were averaged related to the onset of each beat cycle $t$ (i.e., the nodes of the heating sound) between 20 Hz and 60 Hz. The result showed a brief burst of oscillations with an amplitude peak at 50 ms and dipolar magnetic field distribution above bilateral temporal lobes. The magnetic field was approximated by single equivalent current dipoles in the left and right hemispheres. The head model was a single three-dimensional digitizer (FASTRAK, Polhemus, Colchester, VT). The electromagnetic forward model as implemented in the CTF dipole fit software was used. Dipole sources were estimated for each repeated block, and the means of the dipole coordinates and orientations were taken as individual source model for calculating time series of cortical source activity with the method of source space projection (Ross et al. 2000; Teale et al. 2013; Tesche et al. 1995). All further data analysis was based on the time series of bilateral source activity measured in nano-amp meters. Group mean dipole coordinates were calculated in the head-based coordinate system and transformed into Talairach coordinates by coregistering the three fiducials with a template brain.

**Frequency-domain analysis.** We reported previously a detailed time-domain analysis of the responses to the acoustic beat (Miyazaki et al. 2013). Because of the substantially smaller response amplitudes in case of the binaural beat, such time-domain analysis was not feasible. However, frequency-domain analysis provided highly reliable response measures with excellent signal-to-noise ratio for comparison between the acoustic and binaural beat responses.

The time series of left and right cortical source activities were segmented in 18-s-long epochs, each containing the 16-s sweep of the beat frequency and two additional 1-s intervals before the beginning and after the end of the sweep period. We applied a time-frequency analysis to each single-trial waveform, using complex Morlet wavelets with carrier frequencies between 2 Hz and 80 Hz (Samar et al. 1999). The width of the wavelet, which determines the temporal-spectral resolution, was adjusted to the carrier frequencies to contain two cycles at half-maximum width at 2 Hz and 8 cycles at 60 Hz. The main outcome measure in this study was the phase coherence because it involves a normalization of the spectral amplitudes and accounts for the 1/f low-pass characteristics of the MEG spectrum by equally weighting all frequency components in the range of interest. This choice of data analysis was specifically important for this study to attain a fair comparison between the brain responses across the relatively wide spectral range. The phase coherence can be interpreted as a metric of how much of the ongoing brain signal has been synchronized with the stimulus. A close relationship between the phase coherence and the signal-to-noise ratio has been shown (Dobie and Wilson 1989). For calculating intertrial phase coherence we used the magnitude-squared coherence algorithm (Dobie and Wilson 1989). For all $N$ trials from repeated blocks we calculated the mean of all complex wavelet coefficients $a(t,f)$ and normalized it by the variance according to

$$PC(t,f) = \frac{1}{N} \sum_{t=1}^{N} a(t,f)$$

in which $a^* (t,f)$ denotes the conjugate of the complex wavelet coefficient. The main difference compared with a more common method of calculating the phase coherence was that the normalization was applied after accumulating mean and variance instead of normalizing each trial (Lachaux et al. 1999). The magnitude-squared coherence considers amplitude information and has been shown to be especially sensitive to auditory evoked oscillatory responses (Dobie and Wilson 1994). One important property of the phase coherence measure is that its statistical distribution under the null hypothesis is known, which directly provides $P$ values for the test. For a large number of trials ($N > 50$), the approximation $P = \exp(-N \times PC^2)$ can be used (Fisher 1996). The number of trials was $N = 120$ for the acoustic beat and $N = 192$ for the binaural beat stimulation for each participant. The complex phase coherence was averaged across participants for calculating the grand averages, and its absolute values were color-coded in time-frequency maps. We also used the time-frequency representation (TFR) of the response as a time-dependent band-pass filter (Bertrand et al. 1994), which was centered at the stimulus frequency at each time.
point, by reconstructing the time series from the wavelet coefficients along the contour of the stimulus beat frequency over time.

Correlation analysis. We applied a correlation analysis between the time series of the sweeping stimulus envelope and the MEG source waveforms to estimate amplitude and phase measures. These measures were then used to compare the left and right hemispheres at various beat frequencies. The correlation analysis was performed in 20 frequency bands with center frequencies \( f_C \) logarithmically spaced between 3 Hz and 60 Hz. Both the time series of the stimulus and the averaged response waveforms were band-pass filtered between \( 0.8 \times f_C \) and \( f_C/0.8 \). The cross-correlation function was calculated between both with the MATLAB signal processing toolbox function xcorr, with time lags in the range of \( \pm 400 \) samples (equivalent to \( \pm 640 \) ms). The time points of the maxima of the cross-correlation provided estimates of the response latency. The phase of the correlation function was measured at the time point of the maximum correlation and compared between left and right auditory cortex. The magnitude of correlation was used for calculating a laterality index \( LI = (\text{right} \text{ - } \text{left})/(\text{right} + \text{left}) \). The laterality index equals 1.0 if the response appears solely at the right side, 0 for equal-magnitude bilateral responses, and -1.0 in the case of a left hemispheric response.

Confidence intervals for all group-mean measures were obtained from bootstrap resampling. For this analysis, the set of participants \((n = 15)\) was resampled 1,000 times and the respective grand average was calculated from the resampled set. The 2.5% and 97.5% percentiles were taken as confidence limits. All analysis was performed with a library of MATLAB functions developed at the Rotman Research Institute.

RESULTS

Behavioral results. Participants detected the acoustic beat almost perfectly up to the beat rate of 60 Hz (Fig. 1). Beyond 60 Hz, the likelihood of judging the sound as beating decreased gradually and reached the 50% level at \( \sim 90 \) Hz. The binaural beat was less certainly detected, even at low frequencies. The detection rate decreased beyond a beat rate of 15 Hz, reached the 50% level at 35 Hz, and asymptotically approached at 65 Hz the level of false positive responses, which was found for the nonbeating tone pairs of equal frequency.

Cortical sources. Localization of equivalent current dipole sources was successful in all participants for the 40-Hz component of the evoked response to the acoustic beat. Mean dipole locations in the head-based coordinate system were \( x = -7.0 \) mm, \( y = -49.8 \) mm, \( z = 58.3 \) mm for the right hemisphere and \( x = -10.8 \) mm, \( y = 50.7 \) mm, \( z = 57.1 \) mm for the left hemisphere, corresponding to Talairach coordinates of the MNI-colin27 template brain of \( x = -45 \) (right), \( y = 22 \) (posterior), and \( z = 13 \) (superior) in the right hemisphere and \( x = 51 \), \( y = 23 \), \( z = 10 \) in the left hemisphere. The auditory sources in the right hemisphere were \( 6 \) mm more anterior than those in the left hemisphere \((t(14) = 5.5, P < 0.001)\), which is characteristic for the asymmetry of auditory cortices (Penhune et al. 1996) and demonstrates the reliability of the source estimation.

Time-frequency representations. Figure 2 provides an overview of the stimulus-evoked responses in the time-frequency domain. The acoustic beat elicited responses predominantly at the beat frequency. Figure 2A shows the concentration of the response around the bell-shaped white line, which indicates the time course of the stimulus sweep in the TFR. In addition, acoustic beat responses occurred at integer multiples of the beat frequency, again indicated as concentration along the trajectories of 2, 3, 4, and 5 times the beat frequency in Fig. 2A. Responses were especially expressed at low frequencies \((<10 \) Hz) and at \( \gamma \)-frequencies \((30–60 \) Hz). The binaural beat elicited generally smaller responses indicated by lower phase coherence values (Fig. 2B). The binaural beat response was especially dominant in the \( \gamma \)-band, as clearly noticeable in the TFR.

Rearranging the \( x \)-axis of the TFR according to the beat frequency instead of the time resulted in the time-frequency maps shown in Fig. 3 for the acoustic beat. The responses obtained with the upward sweep between 3 Hz and 60 Hz and the downward sweep were averaged separately for the left and right auditory cortices. A cross section of the time-frequency maps at 40 Hz is shown in Fig. 3, top. It indicates that a 40-Hz response was elicited not only by the 40-Hz beat but also at 20 Hz, 14 Hz, and 10 Hz. Moreover, the overlay of responses obtained during up sweep and down sweep illustrates that the response sizes were largely independent of the sweep direction. The \( \gamma \)-band responses appeared to be larger right compared with left. Measuring the response magnitude at the beat frequencies, which are the response magnitudes along the diagonal in the time-frequency maps in Fig. 3, A and B, results in the beat transfer characteristics shown in Fig. 3C. The transfer characteristic for the acoustic beat showed maxima at low frequencies \((\leq 3 \) Hz) and around 12 Hz and the largest maximum at 40 Hz, as well as minima at 8 Hz and 20 Hz, for both the left and right responses. The thin lines in Fig. 3C indicate the 95% confidence limits for the group means. The confidence intervals include the mean magnitude of the contralateral hemisphere across the beat frequency range, except in the 40-Hz range. This indicates significantly larger 40-Hz responses in the right hemisphere than in the left hemisphere.

Similarly arranged time-frequency maps of the phase coherence for the binaural beat demonstrate most prominent responses in the 30–60 Hz \( \gamma \)-frequency range (Fig. 4, A and B). However, the response magnitudes were clearly smaller than for the acoustic beat. The beat transfer function (Fig. 4C) showed noticeable differences between responses in the left and right auditory cortex. The response was significantly greater in the left hemisphere at beat frequencies around 6 Hz and in the right hemisphere at around 15 Hz. In contrast to the acoustic beat, no hemispheric difference was obvious for the binaural beat in the 40-Hz range.

Fig. 1. Group mean behavioral results of identifying the stimuli as beating sound. Whereas the acoustic beat was perceived at beat rates up to 60 Hz, the ability to identify the binaural beat decreased above 15 Hz. Dashed line equals \% of false positive responses to equal-frequency nonbeating tones. Error bars denote 95% confidence limits for the group mean.
Response time series. Time courses of the group mean acoustic and binaural beat responses are shown in Fig. 5A. The wavelet filter, which was effectively a time-varying band-pass filter with the center frequency adjusted to the beat frequency, resulted in clean waveforms of the oscillating response at the beat frequency. Both types of beat responses show large-magnitude fluctuation across the frequency range between 3 Hz and 60 Hz, and the fluctuations were rather different for the acoustic and binaural beats. A common property of the time series was the response maximum at 40 Hz. Another difference between the acoustic beat and the binaural beat was revealed when the responses from the left and right auditory cortices were compared. Fig. 2. Group mean time-frequency representations (TFRs). A: TFR for the phase coherence of responses to the acoustic beat. The time axis spans the 16-s interval of sweeping the beat frequency between 3 Hz and 60 Hz and back. Bell-shaped white lines indicate the trajectories of the beat frequency $\Delta f$ and 2–5 times $\Delta f$, as indicated by the numbers on top of the TFR. Most prominent is the response following the trajectory of $\Delta f$, with maxima at low frequencies and in the $\gamma$-frequency range. In addition, responses occurred at multiples of $\Delta f$, especially at $\gamma$-frequencies. B: TFR for the responses to the binaural beat, which were of smaller magnitude but clearly expressed at low and $\gamma$-frequencies.

Fig. 3. TFR for the acoustic beat response. A: the TFR shown in Fig. 3 was reorganized according to the beat frequency for the left auditory cortex. The trajectory of the beat sweep appears in the main diagonal. Responses to both sweep directions were averaged. Top graph demonstrates that for the response at 40 Hz the upward sweep and the downward sweep resulted in similar response amplitudes. The 40-Hz response shows peaks at 10-Hz, 14-Hz, 20-Hz, and 40-Hz beat stimulation. B: the TFR for the right auditory cortex shows larger response amplitudes at $\gamma$-frequencies. C: transfer characteristics for the acoustic beat response obtained by taking the amplitude along the diagonal in A and B. Thin lines indicate the 95% confidence limits for the group mean, indicating significantly larger amplitudes around 40 Hz in the right auditory cortex.
right auditory cortices were overlaid, which is shown for three selected frequencies of 3 Hz, 40 Hz, and 60 Hz in Fig. 5B. Whereas the phases of the bilateral time series were exactly aligned for the acoustical beat, the binaural beat responses showed systematic phase differences between left and right auditory cortices. Specifically at 3 Hz, the bilateral responses were of almost opposite polarity. The phase differences were significant, as indicated by nonoverlapping 95% confidence intervals for the group mean phase (Fig. 5C). At 3 Hz, the left hemispheric response was leading by almost 180°, while in the right hemispheric response was leading by almost 120°.

**Cross-correlation analysis.** More detailed information about the hemispheric phase relations was obtained with a cross-correlation analysis of the stimulus beat and the brain responses, summarized in Fig. 6. The analysis revealed that the phases of bilateral time series were exactly aligned for the acoustical beat, the binaural beat responses showed systematic phase differences between left and right auditory cortices. Specifically at 3 Hz, the bilateral responses were of almost opposite polarity. The phase differences were significant, as indicated by nonoverlapping 95% confidence intervals for the group mean phase (Fig. 5C). At 3 Hz, the left hemispheric response was leading by almost 180°, while in the right hemispheric response was leading by −120°.

**Hemispheric asymmetry.** The hemispheric differences in response magnitude and phase are summarized in Fig. 8. Whereas the bilateral phases were confined within a ±20° band across the entire frequency range for the acoustical beat, the binaural beat responses were of almost opposite polarity at 3 Hz (Fig. 8A). The binaural beat phase difference changed gradually with increasing frequency to −120° at 10 Hz and remained constant at this phase difference for the beat range from 10 Hz to 60 Hz. The almost constant phase over this frequency range suggests that the cross-hemispheric relationship is defined by the phase and not by a certain delay time.

The different hemispheric phase relationships for the acoustical beat and the binaural beat are illustrated with the spatial maps of the magnetic field response at 3 Hz in Fig. 8B. In the case of the acoustical beat the spatial map showed patterns of two dipolar distributions above the left and right temporal lobe, which are characteristic for auditory cortex sources of same polarity. In contrast, the topographic map for the binaural beat response showed dipolar maxima at similar places but the right and left hemispheric dipoles showed opposite orientations.

The hemispheric balance of the response magnitude was expressed with the laterality index, visualized in Fig. 8C. The acoustical beat response showed symmetric response magnitudes up to 20 Hz and more right-lateralized responses in the 30- to 60-Hz γ-frequency range. The binaural beat response showed a strong left lateralization around 6 Hz, right lateralization around 15 Hz, and symmetric responses in the γ-frequency range. These patterns were consistent between upward and downward sweeps.

**Response phase at low frequency (3 Hz).** At low beat frequencies, the dichotically presented two-tone stimuli induce the illusion of a moving sound rotating back and forth between left and right ears. We showed that in this case the responses were of opposite polarities in the left and right auditory cortices. The temporal relationship between the stimulus and the brain response at 3 Hz is visualized in Fig. 9. While the IPD increases continuously over time, wrapping the phase around the interval (−π, π) results in a sawtoothlike time course of the IPD (Fig. 9D). However, lateralization of the 500-Hz sound is maximal around 0.5π and crosses the midline smoothly at
equal and opposite bilateral phases (Domnitz and Colburn 1977). Therefore we approximated the time course of the IPD by the sine wave of its first-order Fourier expansion to obtain an estimate of the perceived lateralization (colored graph in Fig. 9 D). At the maxima of this sine wave, the ITD was ±0.5 ms, equivalent to a quarter of the cycle of the 500-Hz sound, which is close to the physiological period of ±0.6 ms, corresponding to an acoustic wavelength equal to the size of the human head. We compared this time series of the IPD stimulus (Fig. 9D) with the grand-averaged auditory cortex responses observed from the correlation analysis (Fig. 9E). The latency between the time point of maximally left localization of the stimulus and the time point of the response maximum in the contralateral right auditory cortex was 83 ms in mean. The responses in bilateral auditory cortices were of opposite polarity and reached maximal amplitudes after a delay with respect to the assumed time point of maximal sound lateralization.
DISCUSSION

We report human auditory cortex responses to acoustic beat and binaural beat stimuli over the physiologically relevant range of beat frequencies. We found that the response amplitudes and phases fluctuated across the beat range, which suggests different underlying brain processes in different frequency bands. This calls for separate discussions of the different frequency bands. While responses were maximal in the \( \gamma \)-band for both types of stimulation, the binaural beat responses were generally smaller than the acoustic beat responses. Differences between binaural and acoustic beat responses were most strongly expressed in interhemispheric phase differences. We found bilateral phase differences for the binaural beat, while the acoustic beats elicited responses with equal phase in the left
and right hemispheres. Specifically at the lowest frequency of 3 Hz, the binaural beat responses were of opposite polarity, supporting the hypothesis of sound localization encoding through bilateral asymmetry in the central auditory system.

**Behavioral results.** Although our behavioral test procedure was relatively simple, the obtained transfer characteristics agree with the literature. Performance on the acoustic beat detection task showed a low-pass characteristic comparable to known amplitude modulation transfer characteristics (Viemeister 1979). Fast binaural processing with an upper frequency limit similar to that for AM detection has been shown with noise stimuli containing fast interaural phase transitions (Siveke et al. 2008). However, we found a noticeably lower cutoff frequency for the binaural beat. The performance was best between 10 Hz and 15 Hz, decreased for higher frequencies, and reached the 50% level at ~30 Hz, which is consistent with earlier reports (Perrott and Nelson 1969).

The different low-pass characteristics for binaural and acoustic beat perception have previously been taken as indication for lower temporal acuity in the binaural system compared with the monaural system. However, for a fair comparison one must consider the significantly reduced salience of the binaural beat compared with the acoustic beat for equally intense two-tone complexes (Grose et al. 2012). When manipulating the phase characteristics of noise stimuli, which largely overcomes the saliency problem, similar characteristics have been found for both the monaural and binaural systems, suggesting that they have similar temporal acuity (Siveke et al. 2008).

**Previous event-related potential literature.** Previous reports of binaural beat responses may appear to be inconsistent, as

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**Fig. 7.** Response latency estimated from the maxima of cross-correlation between the stimulus beat and the response. Shaded areas indicate 95% confidence intervals for the group means.

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**Fig. 8.** Phase and amplitude balances between left and right hemispheres. A: group mean phase difference between left and right auditory cortex source activities. Dotic stimulation, which generates acoustic beating, elicited phase-aligned cortical responses. Phase differences were <20° across the frequency range. Error bars indicate 90% confidence intervals for the group mean. The binaural beat in case of dichotic stimulation causes phase differences between left and right hemispheres. At low frequencies the right hemisphere is leading by close to 180°. Between 10 Hz and 60 Hz, the left hemispheric response is leading by 120°. B: topographic maps of the MEG at 3 Hz show 2 dipolar pattern above the temporal lobes, characteristic for auditory cortex sources. Arrows indicate underlying the dipoles with same polarity. In the case of the binaural beat, the dipoles are of opposite polarity. C: the amplitudes of responses to the acoustic beat were balanced between hemispheres below 20 Hz and showed a right hemispheric preference in the gamma-frequency range. The response amplitudes elicited by the binaural beat were strongly left lateralized around 6 Hz and right lateralized around 15 Hz. They were, however, balanced at low frequencies and in the gamma-band.
Pratt and colleagues (2010) lamented. For example, regarding response lateralization, studies reported symmetric bilateral responses (Karino et al. 2006), right lateralization (Draganova et al. 2008), and left dominance of the binaural beat response (Pratt et al. 2009). In our opinion, the apparent disagreement likely resulted from comparison of different experimental conditions, notably different beat rates. The strength of the present study is that we provide the first coherent report of binaural beats across a wide beat range. In fact, we found that the response properties changed strongly across the frequency range between 3 Hz and 60 Hz, which was not evident from observations at only a few samples of the beat frequency in the early studies.

The first EEG study about steady-state responses to binaural and acoustic beats used a beat rate of 40 Hz and stimulus frequencies around 400 Hz and 3,200 Hz (Schwarz and Taylor 2005). Whereas acoustic beat responses were elicited with low- and high-frequency sounds, a binaural beat response was detectable at 400 Hz but not at 3,200 Hz, which is consistent with the finding that cortical responses to ITD changes are limited to the frequency range below 1,500 Hz (Ross 2008; Ross et al. 2007b). Other studies used lower frequencies only. Still, response amplitudes were smaller at 1,000 Hz than at 250 Hz (Pratt et al. 2010). Binaural beat responses were consistently recorded with a 390/430-Hz tone pair. However, no response was detectable with an 810/850-Hz tone pair in most of the same participants (Grose and Mamo 2012). The finding in the latter study, that simultaneously recorded frequency-following responses were strongly attenuated for the higher-frequency stimuli, supports the hypothesis that neural synchronization with the stimulus carrier at the brain stem level is required for binaural processing.

The first MEG study of the binaural beat showed small but significantly detectable responses to 4-Hz and 6.66-Hz binaural beats at stimulus frequencies of 240 Hz and 480 Hz (Karino et al. 2006). Although multiple sources were suspected, the most prominent responses were localized in bilateral temporal areas around the primary auditory cortex. Phase measures were variable and not consistent across stimulus conditions. Our present data revealed a phase transition in the 4-Hz to 6.66-Hz interval (Fig. 8A). This frequency interval corresponds to the perceptual transition between perceiving dominantly a moving sound at lower frequencies and loudness fluctuations for beat frequencies above 5 Hz. We observed left-lateralized responses around 6 Hz and more balanced bilateral responses at 4 Hz. Because of this dependence on the beat frequency, a consistent pattern of amplitude and phase measures could not be obtained from previous observations at two frequencies only.

In MEG, significantly larger 40-Hz auditory cortex responses in the right hemisphere have been reported for both binaural beats and acoustic beats (Draganova et al. 2008). Our present data showed considerably larger right hemispheric
responses for the acoustic beat as we showed before for AM sounds (Ross et al. 2005), while the binaural beat responses were not asymmetric between hemispheres. Our finding that bilateral 40-Hz response phases were identical for the acoustic beat but differed by ~90° for the binaural beat is consistent with previous reports by Draganova et al. (2008).

In summary, the apparent inconsistencies across previous studies from different laboratories can be explained by a close look at the frequency characteristics of the beat responses. It is important to note that several previous studies to binaural and acoustic beats share common characteristics and suggested common underlying neural mechanisms for low-frequency (Pratt et al. 2010) and 40-Hz (Draganova et al. 2008) responses. However, investigating the responses across a wide frequency range revealed characteristic differences between both types of responses in addition to commonalities. In the following section we consider separately response characteristics in the different frequency regions.

It would be desirable to correlate responses at various beat rates with behavioral findings. However, given the small response amplitudes we could report results on the level of group averages only and compare those to behavioral findings reported in the literature. Future work is required to focus on brain responses and behavioral performances at distinct beat rates.

Responses at low beat rates—sound localization. Two perceptual phenomena emerge at low beat rates: the bilateral tones fuse into a single tone, and this tone is localized as moving periodically between the left and right ears. The upper limit for perception of such a “rotating tone” has been described as Δf equal to 5–10% of the tonal frequency (Perrott and Musicanet 1977) or as the absolute value of 5 Hz (Blauert 1972; Grantham and Wightman 1978). Although we did not test the perceptual quality explicitly, we assume that our lowest beat rate of 3 Hz was capable of inducing the illusion of a moving sound. We recorded brain responses evoked by slowly changing beats in the 3-Hz range for >2 s in each trial. This resulted in a sufficiently large number of epochs for signal averaging to obtain clear responses.

The binaural beat response in the 3-Hz range was characterized by balanced bilateral amplitudes of opposite polarity, while the acoustic beat elicited bilateral responses with equal polarity. Previous EEG recordings may have missed the phase differences because the dipolar potential patterns from left and right auditory responses overlap in frontal central areas. The overlapping signals with opposite polarity, typically close to temporal T5/T6 electrodes, may not have had a large enough signal-to-noise ratio to allow for a reliable phase comparison (Pratt et al. 2010).

We interpret our finding of opposite phases in left and right auditory cortices in the context of cortical representation of sound localization through asymmetry of the magnitudes of cortical responses between hemispheres. Evidence for such opponent-channel coding of ITD in humans has been concluded from using stimuli that elicited responses specific for ITD transitions. The opponent-channel model predicts larger responses for an outward location shift from central to lateral. Accordingly, larger EEG responses to outward ITD changes compared with inward changes have been found (Magezi and Krumholz 2010). Our low-frequency finding of a steady-state response that continuously follows the ITD changes of periodically moving sound reflects the principle that cortical responses are largest contralateral to the lateralized sound.

The response latency was on the order of 100 ms, which may suggest a relationship to the sensory evoked P1-N1-P2 response. The evoked response signals a change in the acoustic environment and is likely involved in the encoding of single auditory objects (e.g., as in speech and music). The time constant of 200 ms for temporal integration in this auditory process defines the trade-off between perception of single events and an auditory stream (Yabe et al. 2001) and may apply to identification of the sound location in an analogous way. Thus the time constants of auditory analysis and interpretation effectively limit the perception of moving sound items, while the binaural system itself may resolve much finer timescales.

40-Hz γ-responses—binaural temporal modulation. Large 40-Hz responses for both the acoustic and the binaural beat were outstanding findings in this study. However, the sharply tuned frequency characteristic seems not to be compatible with present and previous behavioral findings. The acoustic beat was equally well perceived for low frequencies including 40 Hz. In contrast, detection performance for the binaural 40-Hz beat was close to chance level. Then how can we explain the dominance of the 40-Hz response? First, it is noteworthy that single-unit recordings of binaural beat responses showed that cortical neurons do not fire particularly at rate of 40 Hz. In anesthetized cats the cortical spike rate increased with increasing binaural beat rate, reached a maximum at 13 Hz, and decreased continuously for higher rates (Reale and Brugge 1990). The highest beat rate in that study was 45 Hz, and no increase in the spike rate was observed around 40 Hz. Notably the spikes in the 40-Hz range were strictly phase-locked to the beat cycle, which was not the case at other frequencies.

Anesthesia could have caused a suppression of the 40-Hz responses. Indeed, in anesthetized macaque predominantly transient responses were found, whereas sustained neural firing was observed in the alert animal (Scott et al. 2009). In that study, the spike rate was largest around 10 Hz and showed low-pass characteristics with reaching the 50% level at 20 Hz, and no specifically larger binaural beat response was found around 40 Hz.

Predominant MEG responses at 40 Hz more likely reflect a general mechanism of cortical processing. Intracellular recordings in cat revealed that fast-spiking interneurons in superficial and deep cortical layers are the main sources for 40-Hz oscillations in cortico-thalamic networks (Steriade et al. 1998). The role of 40-Hz γ-oscillations for neural communication based on synchronization and phase coding has been conceptualized (Womelsdorf et al. 2007) and has been proposed as the neural mechanism underlying sensory binding and object representation for conscious perception (Bertrand and Tallon-Baudry 2000; Engel and Singer 2001). Recent experimental findings from an optogenetic study supported those concepts: When fast-spiking interneurons in barrel cortex in mice were synchronized with laser-light pulses at 40 Hz, neurons were sensitive to concurrent whisker stimuli at a specific phase of the γ-cycle and sensory response timing was most precise at this phase (Cardin et al. 2009). Consistent with the concept that γ-oscillations modulate the synaptic input of cortical neurons is the fact that the EEG and MEG signal is mainly generated by...
postsynaptic current flows in the apical dendrites of large pyramidal cells in layer IV–VI of the cortex (Lopes Da Silva 2004). Thus a reasonable assumption is that the 40-Hz MEG reflects postsynaptic oscillations that sharpen the timing of cortical neurons and thus control sensory processing and perceptual binding.

In our study, 40-Hz oscillations were strongest when the stimulus beat rate was also 40 Hz. However, partials of 40 Hz (20 Hz, 14 Hz, 10 Hz, etc.) elicited 40-Hz responses also, at least for the acoustic beat. In our previous analysis of the temporal structure of responses to the acoustic beat, we found that each beat elicited a short wave of 40-Hz oscillations at lower beat rates (Miyazaki et al. 2013). Our time-frequency analysis of the acoustic beat responses showed that the responses strength doubled when the beat rate increased from 20 Hz to 40 Hz, which could be explained by the effect of temporal integration across twice as many beats at 40 Hz compared with 20 Hz. Both our analyses in the time domain and in the frequency domain agree that each acoustic beat elicits a burst of 40-Hz oscillations, and the superimposition results in the strongest response at 40 Hz. Nonetheless, superimposition of a 40-Hz burst to each beat cycle does not completely explain the predominant 40-Hz activity, and likely further synchronization of intrinsic oscillations contributed to the response (Ross et al. 2012). Our finding that stimulation at integer fractions of 40 Hz synchronized 40-Hz oscillations suggests that stimuli at any frequency elicited responses. Responses were exceptionally large and best observable at 40-Hz simulation.

When comparing the time-frequency maps for the acoustic beat and the binaural beat, it seems reasonable to assume a common mechanism for the generation of oscillations. However, the amplitude for the binaural beat was smaller than for the acoustic beat, and we could not detect a prominent 40-Hz response with the 20-Hz or 10-Hz binaural beat. This is essentially a matter of sufficient signal-to-noise ratio, which could be obtained with substantially increased measurement time. The amplitude of the 40-Hz steady-state response to AM sound depends strongly on the modulation depth. Given that the salience of the binaural beat stimulus corresponds to an AM sound of ~5% modulation, we would expect only 20% of the amplitude observed for a fully modulated AM sound of the same intensity (Ross et al. 2000), which is consistent with the reduction of the 40-Hz binaural beat response compared with the acoustic beat response in the present study and previous reports (Draganova et al. 2008; Schwarz and Taylor 2005).

If the phase of oscillations provides a mechanism for precise timing and synchronization of neural firing within the cycle (i.e., 25 ms) (Singer 2009), faster stimuli would cause ambiguity in such a coding schema. Therefore, the rhythm may reflect the upper limit for temporal processing in the cortex. Our behavioral finding of the frequency characteristics for perception of the acoustic beat as well as previous reports of the temporal modulation transfer functions for AM detection show low-pass characteristics with corner frequencies in the range, which is consistent with the concept of a temporal processing limit at frequencies.

Asymmetry in interhemispheric phases. Besides different amplitudes, we found significant asymmetries in bilateral phases. Over a wide frequency range between 10 Hz and 60 Hz, the binaural beat response showed a phase difference on the order of 90° compared with aligned phases for the acoustic beat. This is a very unique finding. The topographic map of the evoked magnetic field of the bilateral dipolar pattern as found for the acoustical beat has been shown in hundreds of auditory MEG studies and reflects common timing of bilateral responses for monaural and binaural stimulation. Out-of-phase binaural beat responses strongly contrast the common findings. Even for completely lateralized sounds, no latency differences were found in the auditory evoked MEG response (Woldorff et al. 1999).

Differences in response latency have been proposed as a neural code for simultaneous processing of concurrent objects (Oram et al. 2002). Oscillations with 90° phase difference, as observed over a wide range of beat frequencies, may be especially suitable for such encoding because the responses are orthogonal and therefore most independent. Following this concept, one can assume that separate representations of the auditory input exist in bilateral auditory cortices in the case of the binaural beat.

The hemispheric amplitude asymmetry, with predominant amplitudes around 6 Hz left and 15 Hz right, may further contribute to separate auditory cortex representations in binaural hearing. Although the present findings were consistent with previous reports, the specific role of the response laterality needs further investigation. Different time constants for processing in the left and right auditory cortex have been found, and preferences for processing temporal information have been suggested. However, hemispheric lateralization may also depend strongly on the actual experimental procedure and may even be modulated by the stimulus context through top-down mechanisms (Schönwiesner et al. 2007). Binaural beat responses in the 6–15 Hz range were small and variable between participants and hence less accessible to interpretation compared with the low-frequency responses. Our analysis of the low-frequency responses revealed an opponent-channel code for sound localization and oscillation, which suggests a temporal code for separation of binaural sound representations.

In brief summary, we would like to emphasize three key findings of our study. First, the opposite polarity of binaural beat responses at low frequencies supports the hypothesis of opponent-channel encoding of sound localization in bilateral auditory cortices. Second, phase differences between left and right auditory cortex responses suggest separate bilateral auditory representations, supporting the roles of auditory cortices for binaural hearing based on the temporal structures of sound. Third, 40-Hz oscillations evoked by all binaural transients may reflect a neural mechanism for precise response timing rather than a correlate of perceptual performance.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).
AUTHOR CONTRIBUTIONS

Author contributions: B.R., T.M., J.T., and T.F. conception and design of research; B.R. and S.J. analyzed data; B.R., T.M., J.T., S.J., and T.F. interpreted results of experiments; B.R. prepared figures; B.R. drafted manuscript; B.R., T.M., J.T., S.J., and T.F. approved final version of manuscript; T.M. and J.T. performed experiments; T.M., J.T., S.J., and T.F. edited and revised manuscript.

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