Chapter 32
Cochlear Contributions to the Precedence Effect

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Abstract Normal-hearing individuals have sharply tuned auditory filters, and consequently their basilar-membrane (BM) impulse responses (IRs) have durations of several ms at frequencies in the range from 0 to 5 kHz. When presenting clicks that are several ms apart, the BM IRs to the individual clicks will overlap in time, giving rise to complex interactions that have not been fully understood in the human cochlea. The perceptual consequences of these BM IR interactions are of interest as lead-lag click pairs are often used to study localization and the precedence effect. The present study aimed at characterizing perceptual consequences of BM IR interactions in individual listeners based on click-evoked otoacoustic emissions (CEOAEs) and auditory brainstem responses (ABRs). Lag suppression, denoting the level difference between the CEOAE or wave-V response amplitude evoked by the first and the second clicks, was observed for inter-click intervals (ICIs) between 1 and 4 ms. Behavioral correlates of lag suppression were obtained for the same individuals by investigating the percept of the lead-lag click pairs presented either monaurally or binaurally. The click pairs were shown to give rise to fusion (i.e., the inability to hear out the second click in a lead-lag click pair), regardless of monaural or binaural presentation. In both cases, the ICI range where the percept was a fused image correlated well with the ICI range for which monaural lag suppression occurred in the CEOAE and ABR (i.e., for ICIs below 4.3 ms). Furthermore, the

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lag suppression observed in the wave-V amplitudes to binaural stimulation did not show additional contributions to the lag suppression obtained monaurally, suggesting that peripheral lag suppression up to the level of the brainstem is dominant in the perception of the precedence effect.

1 Introduction

The tuning of human auditory filters (Q_{ERB}), derived from behavioral (tone-on-tone forward masking) and objective methods (otoacoustic emission phase gradient), has been estimated to 12.7, 15.63, and 19.24 for center frequencies of 1, 2, and 4 kHz, respectively (Oxenham and Shera 2003; Shera et al. 2010). Applying a suitable model such as the gammatone filter (Irino and Patterson 1997),

$$\text{BM IR}_{\text{GT}}(t) = at^{n-1}\exp(-2\pi b f_c Q_{\text{ERB}}^{-1} t)\cos(2\pi f_c t + \phi) \quad (t > 0), \qquad (32.1)$$

with parameters $n=4$, $\phi=\pi/2$ and $a=1$, $b=1.018$, leads to a basilar-membrane impulse response (BM IR) description for the human auditory filter. The BM IR durations (i.e., the time until the amplitude reduced by 95 %) calculated from Eq. 32.1 are 18.7, 11.6, and 7.1 ms for frequencies of 1, 2, and 4 kHz, respectively. It is thus expected that BM IRs to clicks that are separated by only several ms will overlap in time. Indeed, already in 1969, Goblick and Pfeiffer observed BM IR interactions in the firing pattern of cochlear nerve fibers in cat in response to temporally spaced acoustical clicks. They described their observations in terms of two systems: an instantaneous compression mechanism and an unknown dynamic compression process.

The present study aimed at characterizing human BM IR interactions noninvasively by using click-evoked otoacoustic emissions (CEOAEs) and auditory brainstem responses (ABRs). Individual correlations between the objective measures and the perception of *monaural* click pairs were performed to determine the contribution of BM IR interactions to the percept of fusion, i.e., the inability to hear out the second click in a click pair (Litovsky et al. 1999). Secondly, the influence of monaural BM IR interactions on the perception of *binaural* click pairs, known to lead to the perception of the precedence effect (e.g., Wallach et al. 1949; Litovsky et al. 1999), was investigated.

2 Materials and Methods

Six normal-hearing subjects with audibility thresholds below 20 dB HL (3 females and 3 males), aged between 24 and 34 yrs, participated in the experiments. All experiments were performed in a double-walled soundproof booth. The 83-μs-long clicks were generated digitally in Matlab with a sampling rate of 48 kHz and were presented over

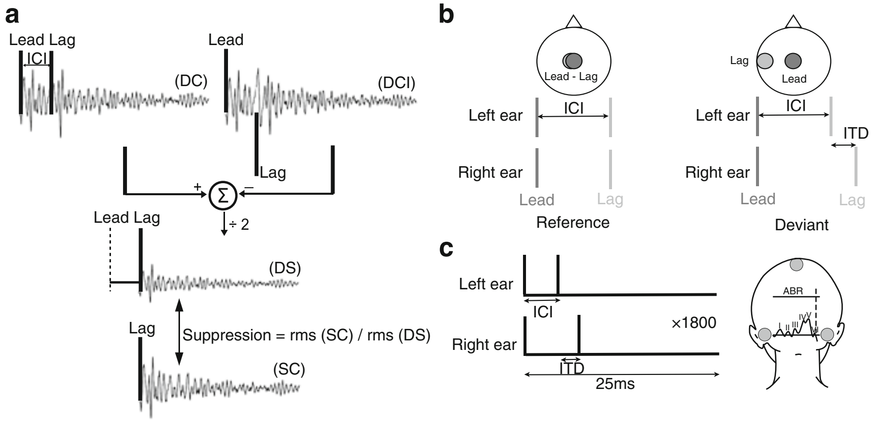

Fig. 32.1 (**a**) Method for obtaining lag suppression in the CEOAE recordings. The stimuli were presented using an interleaved procedure: for each ICI and ITD condition, 1,800 repetitions of the following three stimuli were presented – single click (SC), double click (DC; two condensation clicks), and double click inverted (DCI; one condensation and one rarefaction click). The CEOAE recorded to a DC stimulus contains a CEOAE to the leading click, a CEOAE to the lagging click, and a nonlinear component due to the ICI. To remove the CEOAE to the leading click while maintaining the CEOAE to the lagging click, a derived-suppressed response (DS) was obtained by subtracting the DCI response from the DC response and halving the result (Fig. 1A; Kemp and Chum 1980; Kapadia and Lutman, 2000a, b; Verhulst et al. 2011a). (**b**) Lead-lag click pairs used for the psychoacoustical and objective experiments. For ICIs above the echo-threshold, the reference stimulus leads to a centered percept of two separate clicks, whereas the deviant stimulus leads to a laterized percept to the left for the second click. (**c**) Stimulus configuration for the ABR recordings and visualization of the placement of the Cz, M1, and M2 electrodes

ER-2 earphones (CEOAE and ABR) or Sennheiser HD580 headphones (psychoacoustics). In the left ear, click-pair stimuli were presented at 65 dB peSPL (CEOAE) or 75 dB peSPL (ABR, psychoacoustics) for 7 different inter-click intervals (ICI): 0, 1, 2, 3, 4, 5, and 8 ms. In the right ear, the delay between the clicks corresponded to the ICI in the left ear plus an interaural time difference (ITD) of 300 µs (Fig. 32.1c). The ear-canal recordings were performed binaurally for the CEOAE recordings and both monaurally (L,R) and binaurally for the ABR and psychoacoustical experiments.

Stimulus presentation and data acquisition for the CEOAE recordings were described in Verhulst et al. (2011a). CEOAE lag suppression was calculated as the rms level difference between the derived-suppressed (DS) and single-click (SC) responses in a time frame of 6–18 ms after the onset of the lagging click (see Fig. 32.1b for procedure). The ABR wave-Vs were recorded as described in Bianchi et al. (2013) (Fig. 32.1c). ABR lag suppression was calculated as the wave-V amplitude difference (in dB) in response to the second and the first clicks.

The psychoacoustical echo-threshold (i.e., the smallest ICI at which two separate clicks were perceived) was determined using an adaptive one-interval, two-alternative forced choice (2AFC) procedure. Each trial consisted of a reference and a deviant (Fig. 32.1b) and the subjects indicated whether they perceived one single click (fused image) or two separate clicks (lead and lag). The starting value of the

ICI was 1 ms. After each "single-click response," the ICI was increased, and after each "two-click response," the ICI was decreased. The initial step size was 1 ms and was reduced to 0.5 and 0.3 ms as the threshold was approached. The echo-threshold was obtained after six reversals and corresponded to the 70.7 % point on the psychometric function. Thresholds were obtained as the average of three repeated experimental runs. Additional experiments investigating the laterization of the click pairs used here were performed in Bianchi et al. (2013) for the same subjects.

3 Results

3.1 Monaural BM IR Interactions

Monaural lag suppression, representing the level difference between the CEOAE to a single click (SC) and the lag CEOAE derived from the CEOAE to a lead-lag click pair (DS; see Fig. 32.1a), is shown in Fig. 32.2a as the mean over six subjects. Lag suppression was observed for ICIs up to 8 ms. Maximal suppression with individual levels up to 10 dB was found for ICIs of 1–2 ms, in agreement with earlier studies (Kapadia and Lutman 2000b; Verhulst et al. 2011a). These results demonstrate that the CEOAE to the lagging click in a double-click pair is suppressed with respect to the leading click if the ICI between the lead-lag pair is below 8 ms. Individual results for subject KE were also indicated in panel A, as for this subject, a detailed comparison across methods is shown in panels b and c.

The forward traveling wave to a click excites the whole BM, yet the broadband CEOAE only contains information about local BM processing at those locations where reflections were generated. These locations are observed as components in the CEOAE spectrum, with the strength, number, and frequencies being subject dependent and resulting from the individual BM irregularity pattern (Sisto and Moleti 2008; Shera and Guinan 2007). Figure 32.2b shows a CEOAE spectrum to a single click (i.e., the gray area under SC in all panels) for subject KE, reflecting the broadband nature of the emission. Overlaid in each panel are the spectra of the CEOAE to the lagging click (i.e., the white area under DS) for several ICI conditions. For ICIs up to 2 ms, lag suppression affects all components in the CEOAE spectrum equally, but for larger ICIs, a release from suppression is observed. This release from suppression affects the higher frequencies first as the ICI increases. For an ICI of 5 ms, low-frequency components in the CEOAE are still suppressed, whereas the higher-frequency components show a release from suppression. The frequency dependence of the release from suppression provides a link between CEOAE lag suppression and the local BM IR duration (Verhulst et al. 2011b). Even though it is unclear which exact local BM mechanism is responsible for lag suppression exceeding 6 dB at ICIs larger than zero, BM models based on instantaneous compression can account for the ICI range and frequency dependence of the lag suppression (Kapadia and Lutman 2000a; Harte et al. 2005; Verhulst et al. 2011b).

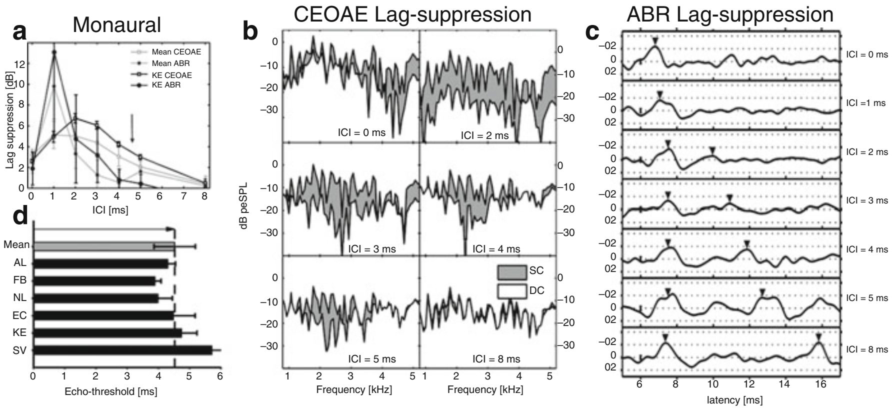

Fig. 32.2 (**a**) Mean and individual levels of monaural lag suppression obtained from CEOAE and ABR recordings. (**b**) Single-click CEOAE (6–20 ms window) spectra for subject KE, overlaid with derived-suppressed CEOAE spectra for different ICI conditions. The noise floor on these recordings is situated around −30 dB peSPL. (**c**) Recorded ABR waveforms to monaural click pairs with varying ICI for subject KE. Wave-Vs are indicated with *triangles*. (**d**) Monaural echo-threshold obtained from monaural stimulation with the reference click pairs in Fig. 32.1b. For ICIs below the threshold, a fused single-click percept was reported for all subjects

The CEOAE lag-suppression results in Fig. 32.2a and b have demonstrated that the amplitude of specific components in the CEOAE to the second click is reduced after the presentation of an earlier click. As CEOAEs predominantly originate from reflections of the forward traveling wave to place-fixed BM irregularities (Zweig and Shera 1995; Shera and Guinan 1999, 2007), it is inferred that these CEOAE amplitude reductions reflect gain reductions in local BM processing. Consequently, there should be correlates of this gain reduction caused by presenting two temporally spaced clicks along the ascending auditory pathway. Figure 32.2c confirms this by showing monaurally recorded ABR waveforms evoked by the reference stimulus in Fig. 32.1b as a function of increasing ICI. Two wave-V components are evoked and reflect activity from the superior olivary complex (indicated with downward pointing triangles; Picton 2011). Whereas the amplitude of the wave-V to the leading click is constant with ICI, the amplitude of the second wave-V increases as the ICI increases. The level difference between the amplitude of wave-V to the leading and the lagging clicks reflects ABR lag suppression and is shown in Fig. 32.2a for subject KE. ABR lag suppression was maximal for an ICI of 1 ms and decreased with increasing ICI. The ICI range of lag suppression was somewhat shorter than the range observed for CEOAE lag suppression, with maximal levels that were up to 5 dB higher for ABR than for CEOAE lag suppression. Even though there may be effects related to inner-hair-cell (IHC) processing and across-channel synchrony that are reflected in ABR lag suppression but not in CEOAE lag suppression, both objective measures exhibit substantial amounts of suppression for ICIs less than 4 ms.

Perceptual correlates of monaural BM IR interactions were investigated with a fusion test (Litovsky et al. 1999; Bianchi et al. 2013), where subjects were asked to report whether 1 or 2 clicks were perceived when listening to monaurally presented click pairs with varying ICIs. For the ICIs where fusion occurs, the leading and lagging clicks are perceived as a single fused event. The results in Fig. 32.1d demonstrate that subjects were unable to detect the second click in a click pair (i.e., perceptual lag suppression) when the ICI was below 4.3 ms. For subject KE, this *monaural echo-threshold* occurred for an ICI of 4.8 ms. ABR and CEOAE lag suppression were always higher below than above this threshold for all subjects tested. This result was significant for all subjects for the CEOAE measure and for 3 out of 6 subjects for the ABR measure (Bianchi et al. 2013).

3.2 Consequences of Monaural BM IR Interactions for Binaural Processing

Given the correlation between objective and perceptual lag-suppression data from Fig. 32.2, this monaural and peripheral component might also affect the perception of binaural click pairs. Binaural click pairs of the deviant type in Fig. 32.1b are known to evoke the *precedence effect* (Litovsky et al. 1999). For ICIs where fusion takes place (i.e., ICIs less than 4.3 ms in this study), a single click at the center of the head was perceived, i.e., at the location of the leading click. When the ICI increased above the echo-threshold, two clicks were heard, with the second click perceived at a location corresponding to the ITD introduced (i.e., to the left for an ITD of 300 μs).

The top panel in Fig. 32.3a shows CEOAE lag suppression obtained for subject KE for the deviant stimuli in Fig. 32.2b. Levels of CEOAE lag suppression were not identical in the two ears. There are two main reasons for this: (1) the frequency content related to the underlying BM irregularity pattern in the CEOAEs was different, and (2) an ITD was introduced in the right ear whereas the left ear only contained an ICI. Nevertheless, both ears demonstrate a substantial amount of BM IR lag suppression for ICIs below 6 ms. ABR lag suppression in the bottom panel of Fig. 32.3a was largest for ICIs below 4 ms. Even though ABR lag suppression was observed for a smaller range of ICIs (0–3 ms) than CEOAE lag suppression (top panel), both objective methods showed suppression for ICIs below 4 ms. The double-click pairs used to evoke the CEOAE and ABRs (Fig. 32.3a) lead to the perception of a fused event in the center of the head for ICIs below 4.8 ms (Fig. 32.3b, KE). Above this *binaural echo-threshold*, the second click in the click pair was lateralized to the left. Individual monaural and binaural echo-thresholds in Figs. 32.2d and 32.3c were similar, in agreement with the fusion thresholds found in Litovsky et al. (1997) and Rakerd et al. (1997). This suggests that lag suppression hinders the perception of the second click, regardless of whether it is presented monaurally or binaurally. The ABR results in Fig. 32.3a furthermore showed *binaural* lag-suppression levels in between the lag-suppression levels obtained for each ear individually

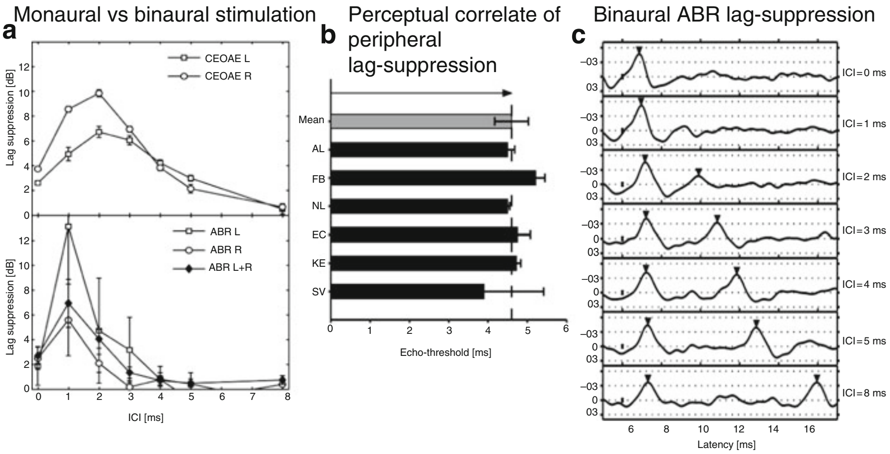

Fig. 32.3 (**a**) Lag suppression obtained from CEOAE and ABR recordings to monaural and binaural stimulation with the click pairs of the deviant type in Fig. 32.1b for subject KE. (**b**) Binaural echo-thresholds for a binaural click pair with ITD of 300 µs. Below the threshold, a single-fused click was perceived, and above the threshold, the second click in the pair was lateralized to the left. (**c**) Recorded ABR waveforms in response to binaural click pairs of the deviant type in Fig. 32.1b for subject KE. Wave-Vs are indicated with *triangles*

(Bianchi et al. 2013). Binaural ABR lag suppression thus seems to reflect monaural lag suppression, as demonstrated in Fig. 32.3c for ABR waveforms recorded to binaural lead-lag click pairs.

4 Discussion

Perceptual consequences of BM IR interactions were investigated by comparing CEOAE, ABR, and perceived lag suppression for lead-lag click pairs in individual subjects. The objective CEOAE and ABR methods showed lag suppression for ICIs below 4 ms. They did not, however, yield identical patterns across ears and methods, which is a consequence of the nature of the signals. Whereas ABR wave-V reflects neural activity across many fibers of cochlear and brainstem sites (Junius and Dau 2005), the CEOAE contains information about those cochlear locations where reflections from the forward traveling wave took place (Shera and Guinan 1999). The CEOAE suppression patterns thus only contain a subset of frequencies (predominantly in the 1–2 kHz region; Puria (2003)) of the synchronously excited region on the BM to a broadband click, leading to higher across-ear-and-subject variability in the CEOAE lag-suppression patterns (Verhulst et al. 2011a). Since release from CEOAE lag suppression is frequency dependent, as observed in Fig. 32.2b, the frequency components in the CEOAE will determine the ICI for which the release of lag suppression is obtained. The higher frequencies contributing to ABR wave-V versus the mid-frequency content in the CEOAE may explain why ABR suppression patterns are generally restricted to shorter ICIs than the CEOAE patterns.

The importance of peripheral processing for the perception of the precedence effect was earlier emphasized by the study of Hartung and Trahiotis (2001), who showed how model predictions based on auditory filtering (gammatone filter bank; e.g., Patterson and Allerhand 1995) and auditory hair cells (Meddis 1986) could account for binaural ITD processing. The results in the present study provide experimental evidence for the proposed bottom-up approach in Hartung and Trahiotis (2001), by showing correlations between CEOAE/ABR lag suppression and the precedence effect. Although it is unclear which cortical or cognitive processes add to the processing of binaural click pairs, the results presented here and in Bianchi et al. (2013) provide evidence for a monaural peripheral contribution to the perception of lead-lag pairs up to the level of the brainstem.

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