Research Article

Perception of Across-Frequency Asynchrony by Listeners with Cochlear Hearing Loss

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ABSTRACT

Cochlear hearing loss is often associated with broader tuning of the cochlear filters. Cochlear response latencies are dependent on the filter bandwidths, so hearing loss may affect the relationship between latencies across different characteristic frequencies. This prediction was tested by investigating the perception of synchrony between two tones exciting different regions of the cochlea in listeners with hearing loss. Subjective judgments of synchrony were compared with thresholds for asynchrony discrimination in a three-alternative forced-choice task. In contrast to earlier data from normal-hearing (NH) listeners, the synchronous-response functions obtained from the hearing-impaired (HI) listeners differed in patterns of symmetry and often had a very low peak (i.e., maximum proportion of “synchronous” responses). Also in contrast to data from NH listeners, the quantitative and qualitative correspondence between the data from the subjective and the forced-choice tasks was often poor. The results do not provide strong evidence for the influence of changes in cochlear mechanics on the perception of synchrony in HI listeners, and it remains possible that age, independent of hearing loss, plays an important role in temporal synchrony and asynchrony perception.

Keywords: synchrony perception, cochlear delays, asynchrony detection, asynchrony discrimination, hearing loss

INTRODUCTION

The perception of timing differences in sounds at different frequencies plays an important role in our ability to parse complex auditory scenes. Sounds that begin and end synchronously are often generated by the same source and should be perceptually grouped, whereas sounds that are asynchronous may come from different sources and so should be perceptually segregated (Bregman 1990; Elhilali et al. 2009). Our perception of timing results from the processing of sound within the auditory system, beginning in the auditory periphery.

Direct measurements from auditory-nerve (AN) fibers of common experimental animals indicate that responses at different places along the basilar membrane (BM) exhibit frequency-dependent delays (e.g., Zerlin 1969; Kim and Molnar 1979; Recio-Spinoso et al. 2005; Siegel et al. 2005; Temchin et al. 2005; Ruggero and Temchin 2007; Temchin et al. 2011). Response delays measured in AN fibers are affected by a delay due to transmission time through the outer and middle ear, a delay due to transmission of mechanical perturbation from the stapes to the place on the BM with the corresponding characteristic frequency (CF), a build-up time of the cochlear-filter response, and synaptic transmission delays between the inner hair cells and the spiral ganglion. Of those delays, the build-up times of cochlear-filter responses dominate the frequency-dependent component of the overall delay (Ruggero and Temchin 2007). In humans, the frequency-dependent cochlear delays have been estimated from noninvasive physiological measurements of latencies of the compound action

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potential (Elberling 1974; Eggermont 1979; Schoonhoven et al. 2001), the auditory-brainstem response (ABR; Eggermont and Don 1980; Neely et al. 1988; Donaldson and Ruth 1993; Harte et al. 2009), and otoacoustic emissions (Neely et al. 1988; Bowman et al. 1997; Schoonhoven et al. 2001; Shera and Guinan 2003; Sisto and Moleti 2007; Harte et al. 2009). Generally, the estimated cochlear-response latency in humans has been shown to decrease with increasing CF at a rate similar to that derived from direct physiological measurements in animals. However, some notable differences between the human and animal data, particularly differences in absolute values of the delays, are still a matter of debate (Shera et al. 2002; Ruggero and Temchin 2007; Shera et al. 2010).

Since the frequency-dependent cochlear delays are dominated by cochlear filtering, the broadening of cochlear filters that often accompanies sensorineural hearing loss may affect the spatiotemporal representation of an input stimulus at the output of the cochlea in more than one way. It has been shown that cochlear damage can lead to spectral smearing and consequently to a loss of spectral information needed for proper identification of speech stimuli, especially in the presence of interfering background sounds (e.g., Miller et al. 1997). Broader filters may also result in shortened response delays in the regions of the cochlea affected by the damage. Indeed, direct recordings from AN fibers have shown that cochlear impairment results in reduced response times (Wang and Dallos 1972; Dallos and Harris 1978; Salvi et al. 1979; Heinz et al. 2010; Scheidt et al. 2010). An important question is whether cochlear hearing loss affects the slope of the cochlear latency–frequency function in ways that may alter the perception of across-frequency timing information.

Recently, Wojtczak et al. (2012, 2013) investigated the perception of relative timing between tones with remote frequencies (i.e., tones exciting remote places on the BM). The studies showed that despite the frequency-dependent cochlear delays, pairs of simultaneously gated tones were judged by listeners with normal hearing (NH) as synchronous on a larger proportion of trials than pairs of tones with any nonzero delay tested (including delays that would be expected to compensate for the difference in cochlear response times for the tones in a pair). The findings were consistent with the hypothesis that differences in cochlear delays across CFs are compensated for at higher-level neural processing stages to produce veridical perception. The hypothesis, if correct, could have different consequences for the perception of relative across-frequency timing information in the hearing-impaired (HI) listeners, depending on the nature of the hypothesized compensating mechanism. A “hard-wired” neural mechanism might remain unaffected by cochlear impairment and thus would provide inadequate compensation for the altered

cochlear delays in the impaired ears. Such inadequate compensation could have perceptual consequences for the processing of temporal information across frequency. In contrast, a mechanism that adapts over time to changes in the peripheral spatiotemporal representation brought about by cochlear damage would facilitate the maintenance of veridical perception of across-frequency timing. Such an adaptation could occur via new neural maps for coding across-frequency timing as a result of repeated exposure to the modified input spatiotemporal representations from the auditory periphery. There are many examples of short- and longer-term sensory plasticity within and across modalities, even in adults (e.g., Hofman et al. 1998), making adaptation to changes in across-frequency cochlear timing a plausible hypothesis.

Before making inferences about the hypothesized compensating mechanism, it is important to consider whether or not damage to the cochlea affects BM-response delays in humans. Studies of the effect of hearing loss, or sound level, on cochlear delays have come to conflicting conclusions. Two studies in which derived-band ABRs were measured in HI listeners with and without Menière’s disease have shown that only the group with Menière’s disease had shorter-than-normal wave-V latencies (Kim et al. 1994; Donaldson and Ruth 1996). Ramotowski and Kimberley (1998) studied the effect of age on cochlear delays estimated using distortion-product otoacoustic emissions. Since the older listeners in their study often had mild high-frequency hearing loss, Ramotowski and Kimberley considered the effect of both age and hearing loss on the delays, but found no significant effect of the latter. In apparent contrast to these studies, Don et al. (1998) found that both absolute BM-response delays and the differences in across-frequency delays, estimated using derived-band ABRs, were shortened in the presence of cochlear hearing loss, but the effect depended on the frequency range. At high frequencies (2.8–5.7 kHz), the delays estimated from the ABR wave-V latencies in HI listeners fell within the range observed for the NH control group. This was true even for listeners with the most severe hearing loss in the high-frequency region (60 dB HL). However, at lower frequencies (0.5–1.4 kHz), a greater hearing loss was associated with shorter estimated BM-response delays. Since there was no change in response delay at high frequencies and the delay decreased with increasing amount of hearing loss at low and medium frequencies, the relative across-frequency delays were progressively reduced with increasing amount of hearing loss in the apical region of the cochlea. Given the data of Don et al. (1998), it should not be surprising that earlier studies (Kim et al. 1994; Donaldson and Ruth 1996; Ramotowski and Kimberley 1998) did not find an effect of hearing loss in listeners without Menière’s disease, since those listeners had predominantly high-frequency hearing

loss (at and above 2 kHz). Some listeners in the study by Kim et al. (1994) had low-frequency hearing loss but a conductive loss (not associated with changes in cochlear-filter bandwidths) could not be ruled out.

The studies discussed above used noninvasive physiological methods to investigate the effect of cochlear damage on BM response delays, but they provide no insight into the effect of hearing loss on the *perception* of relative across-frequency timing information. HI listeners have been shown to exhibit poorer-than-normal performance in several perceptual tasks that rely on across-frequency synchrony such as, for example, comodulation masking release (CMR; Hall and Grose 1989; 1994; Grose and Hall 1996) and intelligibility of two remote bands of tone-vocoded speech (Healy and Bacon 2002; Healy et al. 2005). The poorer performance of the HI has been attributed to a reduced frequency selectivity or/and a reduced ability to integrate across-frequency temporal information. Although changes in frequency selectivity may result in changes in across-frequency cochlear delays, the delays have not previously been considered as a possible distinct contributing factor. To date, no study has explicitly investigated the effect of cochlear hearing loss on the perception of synchrony and the sensitivity to changes in asynchrony between stimuli exciting remote frequency channels. In the present study, psychophysical methods were used to investigate these important perceptual characteristics.

EXPERIMENT 1: SUBJECTIVE JUDGMENTS OF ACROSS-FREQUENCY SYNCHRONY

Rationale

If differences in cochlear delays across CFs are compensated for at higher levels of the auditory system, then this compensation must delay high-frequency components, stimulating the basal regions, relative to low-frequency components, stimulating apical regions in the cochlea, in order to produce synchronous responses to synchronous stimuli. If the putative neural compensating mechanism does not adapt to changes in the cochlea, then increased synchronization of BM responses across CFs in hearing-impaired ears (i.e., reduced differences in across-frequency cochlear delays), due to a broadening of cochlear filters, could result in overcompensation: Perception of synchrony would require delaying low frequencies relative to high frequencies by the amounts by which the across-frequency delays would be reduced in a damaged relative to a healthy cochlea. If, on the other hand, the neural compensating mechanism adapts to changes in relative timing of responses across CFs, veridical perception of the timing should be preserved after cochlear damage, given enough time for the adaptation (plasticity) to

occur. In this experiment, subjective judgments of synchrony between two tones with remote frequencies were made by listeners with cochlear hearing loss, and the data were compared with the results from a similar experiment performed by Wojtczak et al. (2012) using NH listeners.

Stimuli and procedure

A method of constant stimuli was used to measure the perception of synchrony between two tones with remote frequencies as a function of the delay between the tones. Four frequency pairs were tested in separate blocks. Each pair consisted of a 250-Hz tone and a tone with a higher frequency of 1, 2, 4, or 6 kHz. Within a block, the same tone pair was presented with different delays between the tones across trials. A block consisted of 10 random permutations of 17 delays, 0 ms and $\pm 2, 4, 8, 12, 16, 20, 30$, and 40 ms, where the negative sign corresponds to the pairs with the low-frequency (LF) tone leading and the positive delay denotes pairs with a high-frequency (HF) tone leading. The tones had a duration of 40 ms including 10-ms raised-cosine onset and offset ramps. Each tone was presented at a level of 85 dB SPL or 20 dB SL, whichever was higher, to ensure that the tones were clearly audible. Listeners were asked to judge if the tones in a pair were synchronous or asynchronous. All available cues could be used to perform the task, i.e., listeners could base their judgments on the temporal disparity of onsets, offsets, or on the overall duration of the tone pair. No feedback was provided. For each frequency pair, 10 blocks each with 10 different random permutations of the 17 delays were run, resulting in a total of 100 synchrony judgments for each tone pair and each delay between the tones. The tone pairs were presented with a half-octave-wide band of noise centered on the geometric mean of the two tone frequencies. The noise was used to mask the areas of potential overlapping excitation from the tones in order to preclude the use of within-channel cues (such as increments and decrements of excitation level at the output of a channel when the delayed tone was added and the first tone ended, respectively), and thereby to force the listeners to use relative across-channel timing cues. The level of the noise was set to 65 dB SPL. This level was deemed sufficient to mask within-channel cues, as determined based on the outputs of level-dependent gammachirp filters (Irino and Patterson, 1997). The noise was generated in the frequency domain by setting the components of a Gaussian noise outside the desired passband to zero. A new sample of noise was generated for each trial. The tone pairs were temporally centered in the noise waveform. The onset of the noise occurred 400 ms

before the onset of the first tone, and the offset of the noise occurred 400 ms after the offset of the second tone. The noise was gated with 10-ms raised-cosine onset and offset ramps.

To determine tone levels in decibel SPL that corresponded to 20 dB SL, detection thresholds for the 40-ms tones were measured for each frequency used for synchrony judgments, i.e., 0.25, 1, 2, 4, and 6 kHz. Thresholds were measured using a three-alternative forced-choice (3AFC) procedure combined with a two-down one-up adaptive tracking rule that estimates the 70.7 % correct point on the psychometric function (Levitt, 1971). In each trial, two of the intervals contained silence and one interval, chosen at random, contained the test tone (signal). The three intervals, separated by 300-ms silent gaps, were marked by lights on a computer screen. Listeners were asked to choose the interval containing the signal and provided their response via a keyboard or a mouse click. Visual feedback was provided after each trial. A run started with the test tone set to a level that was clearly audible, based on the listener's audiogram. The level was decreased by 8 dB after two consecutive correct responses and increased by the same step after each incorrect response until the second reversal was obtained. After that, the step size was reduced to 4 dB for the subsequent two reversals and to 2 dB for the subsequent eight reversals. A run terminated after a total of 12 reversals were obtained and a single-run threshold was estimated by averaging the levels at the final eight reversal points. The measurement was performed three times for each frequency and the mean of the three single-run thresholds was used as the final threshold estimate.

All the stimuli were generated on a PC, and the experiment was controlled using the AFC software package (Stephan Ewert, University of Oldenburg) under MATLAB (Mathworks, Natick, MA, USA). Stimuli were generated at a sampling rate of 48 kHz using a 24-bit Lynx22 sound card (LynxStudio, Costa Mesa, CA, USA) and were presented monaurally to the left ear using a Sennheiser HD580 headset. The listeners were seated in a double-walled sound-attenuating booth during the testing.

Listeners

Ten HI listeners participated in the study. The listeners' ages ranged from 22 to 75 years with a median of 61.5 years. All the listeners had a sensorineural hearing loss, as indicated by the air-bone gap of <10 dB, a normal tympanogram, and a near-normal performance-intensity function in a speech-recognition test. The listeners had a sloping hearing loss, with low-frequency hearing ranging from normal to mod-

erately impaired. The listeners signed an informed consent prior to their participation and received monetary compensation after each 2-h session. At least one session was devoted to practice. The protocol for all the experiments within this study was approved by the Institutional Review Board of the University of Minnesota.

RESULTS AND DISCUSSION

Thresholds for detecting the 40-ms tones in quiet are shown in Figure 1, with different symbols representing data from different listeners.

Figure 2 shows individual results (symbols) from synchrony judgments. Data for different listeners are shown in different panels. Each plot shows the proportion of "synchronous" responses as a function of the delay between the tones. Different symbols represent the responses for different tone pairs indicated in the legend in the bottom right corner. The last panel in the bottom row shows the mean data obtained from NH listeners in the same task, replotted from the study by Wojtczak et al. (2012).

The intersubject variability in the data was substantially larger for the HI listeners than for the NH listeners in our previous study, with some of the synchronous-response functions exhibiting a plateau on one side, instead of a clearly defined peak (e.g., HI6 for 250 Hz paired with 1 and 2 kHz, HI7 for 250 Hz paired with 4 and 6 kHz, and HI9 for all the tone pairs tested). Such patterns suggest that the percept of synchrony between the tones did not change for these listeners for delays up to at least 40 ms, i.e., up to delays for which there was no longer a temporal overlap between the physical waveforms of the tones in a pair. Because of this surprising result, the conditions were retested multiple times, each time with the same outcome. It should be noted that,

FIG. 1. Thresholds for detecting 40-ms tones for 10 HI listeners.

FIG. 2. Proportion of “synchronous” responses from HI listeners plotted as a function of a delay between the test tones. Different symbols represent data for different frequency pairs indicated in the legend in the bottom right corner. The last panel in the bottom row shows the mean data from six NH listeners, replotted from the study by Wojtczak et al. (2012).

although the listeners did not perceive increasing asynchrony between the tones for one frequency ordering (e.g., LF-tone leading for HI6, and HF-tone leading for HI7 and HI9), their synchronous-response functions had a steep slope for the same tone pairs with the opposite frequency order, indicating that the plateau did not reflect the lack of understanding the task. For each of these listeners, the slopes on the side without a plateau were similar to those observed for the NH listeners in the study by Wojtczak et al. (2012). Additional testing using delays longer than the ± 40 ms in the conditions resulting in plateaus showed that the proportion of “synchronous” responses for these listeners did not drop until the delays between the tones were as long as 80–120 ms (data not shown). After the additional testing with longer delays, the listeners were again retested using the range of delays chosen at the onset of the experiment. The retest yielded very similar results to those shown in Figure 2.

For some of the HI listeners, the synchronous-response functions had a clearly defined peak, but the proportion of “synchronous” responses at the peak was very low, often not reaching a value of 0.5 (e.g., data from HI1–HI3 and from HI5 for 250 Hz paired with 4 and 6 kHz). This result suggests either that the percept of synchrony was not very salient or that the listeners were biased toward choosing the “asynchronous” response.

To estimate the delay corresponding to the maximum proportion of “synchronous” responses, the individual

data were fitted with a model previously used to fit the data from the NH listeners in the study by Wojtczak et al. (2012) and described in the Appendix of that study. The fits, shown by solid curves in Figure 2, were obtained using a maximum-likelihood procedure with binomial distribution (Wichmann and Hill 2001; Dai and Micheyl 2011). The delays corresponding to the peak positions estimated from the fitted curves are shown by the bars in Figure 3, with the negative values indicating that the maximum proportion of “synchronous” responses corresponded to a tone pair with the LF-tone leading and the positive values to a pair with the HF-tone leading.

In the bar plot, the near-zero delays were replaced by a delay of 0.2 ms to make the bars visible (all of them were smaller than ± 0.2 ms). Bars replaced by the arrows indicate conditions where the peak position could not be estimated because of a plateau (the arrows point in the direction of delays for which the plateau was observed). According to the linear model of BM mechanics by de Boer (1980) combined with the Greenwood’s place-frequency map (Greenwood 1990), the response of a healthy cochlea to a 250-Hz tone at its CF would be delayed by 4.3 ms relative to the response to a 1-kHz tone, by 5.4 ms relative to a 2-kHz tone, by 5.9 ms relative to a 4-kHz tone, and by 6.1 ms relative to a 6-kHz tone, at their respective CF places. Assuming an ideal hard-wired compensation for these delays and a complete flattening of the BM latency–frequency func-

FIG. 3. Delays corresponding to the estimated positions of the peaks of the synchronous-response functions. The *positive numbers* indicate that the peaks occurred at delays representing tone pairs with the HF-tone leading, and *negative numbers* indicate peaks at delays representing pairs with the LF-tone leading. The near-zero delays were replaced by a delay of ± 0.2 ms to make the bars visible.

The *arrows* indicate conditions in which the position of the peak could not be reliably determined due to a plateau in the proportion of “synchronous” responses, and the *direction of the arrows* indicates the side of the function with a plateau (down for the side below the peak and up for the side above it).

tion due to hearing loss (i.e., complete elimination of the CF dependence of cochlear delays), these delays with a positive sign (i.e., for a HF-tone leading) can be regarded as representing the expected peak positions for the respective synchronous-response functions. Overall, for the majority of synchronous-response functions, the maximum proportion of “synchronous” responses occurred at positive delays. A one-sample *t* test performed using the delays corresponding to the peaks of all the synchronous-response functions, with the exclusion of the cases denoted by the arrows in Figure 2, showed that across all the HI listeners, the average delay corresponding to the peak (3.1 ms) was significantly >0 ms [$t(31)=5.615$, $p<0.001$]. For the NH listeners in the study by Wojtczak et al. (2012), the delay corresponding to the maximum proportion of “synchronous” responses was 0.6 ms, which was not significantly different from 0 ms. An unequal variance independent-sample *t* test performed to compare the delays corresponding to the estimated peak positions for the HI listeners in this study with those for the NH

listeners in our previous study showed that the delays were significantly greater for the HI than NH listeners [$t(48.239)=4.008$, $p<0.001$]. Assuming that the hearing loss was associated with broader cochlear tuning, the shift of the peak toward positive delays (i.e., pairs with HF-tone leading) is consistent with predictions based on a “hard-wired” neural compensation mechanism that does not adapt to the hearing-loss-induced changes in across-frequency response delays.

The data of Don et al. (1998) suggested that the cochlear latency–frequency function becomes shallower when hearing loss is present at low and medium frequencies, but the function is essentially unaltered by high-frequency hearing loss. Thus, if the results of Experiment 1 indicated overcompensation for reduced across-frequency cochlear delays in the HI listeners, the position of the peak in the synchronous-response function should be positively correlated with the amount of hearing loss in the low-frequency region. Figure 4A shows the relationship between the delays corresponding to the maxima of the synchronous-response functions

FIG. 4. Correlation between thresholds for detecting a 40-ms 250-Hz tone and **A** the delays corresponding to the peaks of the synchronous-response functions, i.e., peak position, and **B** the maximum proportion of “synchronous” responses, i.e., peak height. Different symbols represent data for different frequency pairs. The

filled symbols show data from the HI listeners tested in this study, and the *open symbols* show data from the NH listeners tested in the study by Wojtczak et al. (2012). The *solid line* in each plot represents linear regression.

(i.e., peak positions) for the four frequency pairs tested and threshold for detecting a 40-ms 250-Hz tone, for the 10 HI listeners (filled symbols) used in this study and the 6 NH listeners (open symbols) from the study by Wojtczak et al. (2012). The NH listeners were included because the statistical analyses shown below considered the effect of both listeners' hearing loss and age. Since the youngest HI listener was 22 years old, and all the others fell into the age range between 55 and 75 years, data points from the youngest HI listener could heavily drive the correlations between the tested parameters and age. Some of the NH listeners were older and thus including them resulted in a more continuous age distribution. The Spearman correlation coefficient was computed to test for statistical significance of the relationship between the threshold and peak position, for the peak positions pooled across the four frequency pairs. To avoid an artificial inflation of the number of degrees of freedom due to the inclusion of multiple measurements from the same listeners, the statistical significance of this correlation (and correlations with age described below) was determined using a resampling method: The correlation coefficients were computed 10,000 times in a way that preserved the grouping of observations originating from the same subject. The result yielded an estimate of the distribution of the correlation coefficient under the null (i.e., no correlation) hypothesis, taking into account the correlation structure of the observations. This analysis showed that the peak position of the synchronous-response function was significantly correlated with detection threshold for the 250-Hz tone ($r=0.443$, $p=0.028$). Figure 4B shows the maximum proportion of "synchronous" responses (i.e., peak height) as a function of the detection threshold for the 250-Hz tone. The statistical analysis described above showed that the Spearman correlation between threshold for detecting the 250-Hz tone and the peak height was not significant ($r=-0.317$, $p=0.220$). When the data from the NH listeners were excluded from the analyses, the Spearman correlation between the peak position and

hearing threshold at 250 Hz remained significant ($r=0.461$, $p=0.045$), and the correlation between the peak height and the threshold remained not significant ($r=0.297$, $p=0.377$).

A number of studies have shown that temporal processing deteriorates with age even in the absence of hearing loss (e.g., Fitzgibbons and Gordon-Salant 1994; Strouse et al. 1998; Fitzgibbons et al. 2007). The effect of age has been generally attributed to changes in central neural processing, although some evidence suggests that the effect may have a peripheral component that is not associated with presbycusis. Ramotowski and Kimberley (1998) observed that the latency of distortion product otoacoustic emissions increased with increasing age of the listeners, but there was no correlation between the latency and the listeners' hearing loss. Since most of the HI listeners in this study were older than the NH listeners used in the study by Wojtczak et al. (2012), some of the differences in the perceived synchrony between the two groups of listeners could have been due to the effects of aging on temporal processing. Partial correlations were performed on the data shown in Figure 4A and B, with the listeners' age used as a control variable. After partialling out the effect of age, both the (Spearman) correlation between the 250-Hz threshold and the peak position ($r=0.246$, $p=0.224$) and the correlation with the peak height ($r=-0.070$, $p=0.799$) were not significant. The partial correlations remained not significant when the data from the NH listeners were excluded from the analyses. Because there was a significant correlation between age and threshold for detecting the 250-Hz tone ($r=0.602$, $p<0.001$), the lack of significance of partial correlations needs to be treated with caution. Figure 5 shows correlation between the listeners' age and the peak position (Fig. 5A), as well as age and the peak height (Fig. 5B). The Spearman correlations between the peak position and age ($r=0.378$, $p=0.069$) and peak height and age ($r=-0.380$, $p=0.136$) were not statistically

FIG. 5. Correlation between listeners' age and **A** the delay corresponding to the peak of the synchronous-response function, i.e., peak position, and **B** the maximum proportion of synchronous responses, i.e., peak height. The symbols and solid lines are as in Figure 4.

significant. After excluding the data from the NH listeners, the Spearman correlations between the peak position and age ($r=0.259$, $p=0.281$) and peak height and age ($r=-0.161$, $p=0.640$) were also not significant. Overall, it appears that hearing loss may have affected the peak position, but the peak height was not systematically affected by the listeners' hearing loss at low frequencies or by age.

The synchronous-response functions measured in NH listeners (Wojtczak et al. 2012) consistently exhibited asymmetry about the position of the peak, whereby the slope of the function for tone pairs with the LF-tone leading (below the peak) was significantly steeper than the slope for pairs with the HF-tone leading (above the peak). Figure 6 shows values of the log-transformed unitless model parameter (β) that determined the asymmetry of the solid curves fitted to the data in Figure 2 (for details about this parameter, see the Appendix in Wojtczak et al. 2012). Log values >0 represent functions with a steeper slope below than above the peak (consistent with NH results), while values <0 indicate the opposite asymmetry. Thus, a log value of 0 represents a symmetric shape of the synchronous response function. The asterisks denote cases where the proportion of “synchronous” responses in Figure 2 exhibited a plateau. The position of the asterisk above or below the horizontal line corresponding to the value of 0 indicates on which side of the function the plateau occurred. For comparison, the rightmost set of bars shows the mean log-transformed values of the asymmetry parameter that yielded the best fits to the data from the NH listeners in the study by Wojtczak et al. (2012). While for the NH listeners the slopes were consistently steeper on the side below the peak, some of the HI listeners showed asymmetry in the opposite direction (i.e., shallower slopes below than above the peak). It should be noted that the reversed asymmetry was in most cases associated with a lower maximum propor-

tion of “synchronous” responses (HI1, HI2, HI3, and HI6) and was not consistent across the four frequency pairs (HI1, HI3, HI7, and HI10).

Wojtczak et al. (2012) showed that a model based on signal detection theory (Green and Swets 1966) predicted with high accuracy asynchrony-detection thresholds measured in a 3AFC task from the individual synchronous-response functions, suggesting that the listeners used the same decision rule when performing the subjective-judgment and asynchrony-detection tasks. The experiment below was conducted to examine whether the same modeling approach could be used to predict asynchrony detection in HI listeners and to further examine differences in the perception of the relative across-frequency timing information between the NH and HI listeners by measuring the ability of the HI listeners to detect changes in a delay between asynchronous tones (asynchrony discrimination).

EXPERIMENT 2: ASYNCHRONY DETECTION AND DISCRIMINATION

Rationale

Steeper slopes of the synchronous-response functions for the LF-tone leading (below the peak) than the HF-tone leading (above the peak) in NH listeners were associated with lower thresholds for asynchrony detection with the LF-tone leading than with the HF-tone leading (Wojtczak et al. 2012). The difference between thresholds for the LF- versus HF-tone leading disappeared when listeners had to detect an increase in asynchrony for the baseline asynchronies of 10–20 ms. The synchronous-response functions measured for the HI listeners in experiment 1 did not show a consistent pattern of asymmetry, with some listeners having steeper slopes for pairs with the LF-tone leading, and others having steeper slopes for pairs with the HF-tone leading. These differences in symmetry may predict different (corresponding) asymmetries in

FIG. 6. The log-transformed values of the parameter describing the asymmetry of synchronous-response functions. Positive values indicate a steeper slope below than above the peak of the functions, negative values indicate the opposite asymmetry, and a value of 0 represents a symmetric shape. The asterisks indicate conditions in which plateau was observed on one side of the function. The

position of the asterisks above the x-axis indicates that the plateau occurred for the side above the peak of the synchronous-response function, while the position below the x-axis indicates that the plateau occurred below the peak. The rightmost set of bars shows average values of the log-transformed asymmetry parameter for the NH listeners in the study by Wojtczak et al. (2012).

asynchrony detection depending on listeners' hearing loss and/or age.

Stimuli and procedure

Thresholds for detecting an increase in a delay between two tones were measured as a function of the baseline (standard) delay using an adaptive 3AFC procedure similar to that described for tone detection in experiment 1. The paired frequencies and the duration of the tones, including the duration of onset and offset ramps, were the same as in experiment 1. For each frequency pair, different frequency orders (LF versus HF lead) and different standard delays were tested in random order in separate blocks. On each trial, two intervals contained a tone pair with the same (standard) delay between the tones. The third (signal) interval, chosen at random, contained the same tone pair with a larger delay. The three intervals were separated by 500-ms gaps and were marked by lights on a computer screen. Listeners were asked to choose the interval that sounded different and to provide their responses via a keyboard or a mouse click. Visual feedback immediately followed each response. Three standard delays of 0, 10, and 20 ms were used. Assuming veridical perception of the relative timing between the tones, the listeners performed asynchrony detection for the 0-ms condition and discriminated between different amounts of asynchrony for the 10- and 20-ms standard delays. At the beginning of each run, the delay between the tones in the signal interval was clearly larger than the standard delay. The difference between the delays in the signal and standard intervals ($\Delta ASYNCH$) was decreased by a factor of 2 after two consecutive correct responses and increased by the same factor after each incorrect response until the second reversal was obtained. The factor was decreased to 1.41 between the second and fourth reversal and to 1.19 for the subsequent eight reversals. A run terminated after a total of 12 reversals were obtained. A single-run threshold was computed as a geometric mean of the $\Delta ASYNCH$ values at the last eight reversal points. Three single-run estimates were geometrically averaged to obtain the final threshold. In all conditions, the tone pairs were presented with the half-octave-wide noise bands that were used in experiment 1 to mask within-channel cues. In each trial, the noise started 300 ms before the first interval and terminated with the offset of the tone pair in the third observation interval. The methods for generating the stimuli, the equipment, and the type of presentation (monaural to the left ear) were the same as in experiment 1.

Listeners

The same 10 HI listeners who participated in experiment 1 were recruited for this experiment. The listeners

were given about 1 h of practice using a randomly chosen tone pair to become familiarized with the forced-choice task.

RESULTS AND DISCUSSION

Since the patterns of results differed across the HI listeners, the individual data are shown first before discussing the average data. In experiment 1, synchronous-response functions from some of the HI listeners exhibited a pattern of asymmetry consistent with that observed in NH listeners, while for others, the opposite asymmetry was observed. Because, as shown for the NH listeners by Wojtczak et al. (2012), the side with the steeper slope should indicate a better sensitivity to asynchrony in the LF- or HF-lead condition, the individual data from this experiment were divided into two groups based on the two patterns of asymmetry. For listeners HI1, HI2, HI3, HI6, and HI10, whose synchronous-response functions often had a steeper slope for pairs with a HF-tone leading than with the LF-tone leading (shown by negative values of the log-transformed asymmetry parameter in Fig. 6), asynchrony-detection thresholds, shown in Figure 7, were expected to be lower for the HF-tone leading.

Generally, asynchrony-detection thresholds (for the standard asynchrony of 0 ms) were lower in the HF-lead condition than the LF-lead condition consistent with the expectations. Asynchrony-detection thresholds for listener HI6 were surprisingly low for the 250-Hz tone paired with the 1- and 2-kHz tones in the LF-lead condition since HI6's synchronous-response functions for these tone pairs exhibited plateaus for the LF-tone leading over the entire range of delays tested in experiment 1. Because HI6 was retested multiple times in the task involving subjective synchrony judgments with no effect on the data, it appears that providing visual feedback in experiment 2 may have helped this listener find a more effective cue to detect asynchrony between the tones. When retested in the task involving subjective synchrony judgments without feedback after the completion of the 3AFC task, listener HI6 appeared unable to use the same cue and his subjective data (shown in Fig. 2) remained unchanged.

Figure 8 shows the individual data for the second group of the HI listeners, for whom synchronous-response functions had steeper slopes for the LF-tone leading, consistent with the data of the NH listeners in our previous study.

Unlike for the NH listeners, lower asynchrony-detection thresholds for the LF- than the HF-lead condition were consistently observed across all the four frequency pairs only for one listener, HI4. For the other listeners in this group, there was either no

Fig. 7. Individual asynchrony-discrimination thresholds for five HI listeners whose synchronous-response functions in experiment 1 had steeper slopes above the peak in most conditions. The thresholds are plotted as a function of the standard asynchrony. Blue circles represent thresholds obtained in the LF-lead condition, and red triangles represent thresholds in the HF-lead condition. Different panels show data for different frequency pairs indicated at the top of each column.

consistent trend for order-dependent asynchrony detection or lower thresholds were observed for the HF-lead condition (e.g., data from HI5, and from HI7 for 250 Hz paired with 4 and 6 kHz). Asynchrony-detection thresholds measured from HI9 in the LF-leading condition were surprisingly high given the steep slopes (similar to the mean from the NH listeners) of this listener's synchronous-response functions for the pairs with the LF-tone leading (see Fig. 2).

The model based on signal detection theory presented in the Appendix of the study by Wojtczak et al. (2012) was used to compare thresholds for asynchrony detection predicted from the synchronous-response functions with the thresholds measured in experiment 2. Figure 9 shows log-transformed ratios of the predicted and observed thresholds. The asterisks denote conditions in which the thresholds could not be estimated due to shallow slopes of synchronous-response functions. If the thresholds

were accurately predicted by the model, the log-transformed ratio would be equal to 0. As an example, a log (with a base of 10) ratio of 0.5 indicates that the predicted threshold was more than a factor of 3 greater than the observed threshold. As indicated by the bars in Figure 9, the agreement between the data and model predictions was quite poor, especially (and predictably) for listeners who showed inconsistent patterns of results across the two experiments in this study. Overall, unlike for the NH listeners in our previous study, the results of the HI listeners were often inconsistent across the two tasks, suggesting that many of the HI listeners used different strategies and/or different cues in the subjective and the 3AFC tasks.

Geometric means of thresholds from the 10 HI listeners are shown by the filled symbols in Figure 10. For comparison, thresholds averaged across the NH listeners (open symbols), replotted from the study by Wojtczak et al. (2012) were included in the plots. A repeated-measures ANOVA with factors of tone order

FIG. 8. The same as Figure 7 but for five HI listeners whose synchronous-response functions had steeper slopes below the peak.

(LF versus HF lead), frequency separation, and standard asynchrony was performed on the log-transformed data from the HI listeners, with Greenhouse–Geisser correction applied in cases where the sphericity assumption was violated. In contrast to the results from the NH listeners in our previous study, asynchrony discrimination by the HI listeners showed no effect of tone order [$F(1,9)=2.134$, $p=0.178$] and a significant effect of frequency separation [$F(1.296,11.667)=4.998$, $p=0.038$]. In agreement with the results from the NH listeners, the ANOVA showed a significant effect of standard asynchrony [$F(2,18)=24.534$, $p<0.001$]. Differences between thresholds for the HI and NH listeners were examined by performing an unequal variance independent-samples t test separately for each standard asynchrony and each tone order. The only condition for which the t test showed no significant

difference between the two groups of listeners was the condition with the standard asynchrony of 0 ms (asynchrony detection) for the HF-tone leading [$t(51.058)=-0.858$, $p=0.395$]. The statistical outcome was the same after Bonferroni correction for multiple comparisons was applied. In all the remaining conditions, the HI listeners had, on average, higher (worse) thresholds than the NH listeners in our previous study [0 ms, LF lead: $t(42.398)=-5.594$, $p<0.001$; 10 ms, LF lead: $t(43.854)=-4.431$, $p<0.001$; 10 ms, HF lead: $t(51.102)=-4.450$, $p<0.001$; 20 ms, LF lead: $t(50.467)=-7.252$, $p<0.001$; 20 ms, HF lead: $t(55.693)=-8.377$, $p<0.001$]. Because the HI listeners had worse-than-normal asynchrony-detection thresholds in the LF-lead but not HF-lead condition, the thresholds from the LF-lead condition were correlated with the listeners' age and with absolute thresholds for the 40-ms 250-Hz tone (using the

FIG. 9. Log-transformed ratios of predicted and observed asynchrony-detection thresholds, for the HF-lead (*upper panel*) and LF-lead (*lower panel*) conditions. The predictions were obtained from synchronous-response functions measured in experiment 1 with a model based on signal detection theory, described in Wojtczak et al. (2012). The *different colors of bars*

show the log-transformed ratios for different frequency pairs. The *asterisks* indicate conditions in which predictions could not be obtained. The *negative and positive values* indicate cases where the model underpredicted and overpredicted the observed thresholds, respectively.

resampling method described above) to determine whether either of the two factors was dominant in eliminating the asymmetry that was consistently observed in the data from the NH listeners. The results showed no significant correlation with age ($r=0.288$, $p=0.217$) or with hearing threshold ($r=0.184$, $p=0.436$).

GENERAL DISCUSSION

Cochlear hearing loss and processing of temporal information

Cochlear hearing loss is associated with a decrease in cochlear gain and consequently with elevated hearing thresholds and broadened peripheral auditory filters

(Moore and Glasberg, 1986). Since peripheral filtering is primarily responsible for the frequency-dependent delays of cochlear responses across CFs, broadened cochlear filters may be associated with changes to the slope of the latency–frequency function. To our knowledge, no earlier psychophysical study has explicitly addressed the effects of cochlear hearing loss on the perception of across-frequency synchrony, but a number of studies have investigated the effect of hearing loss on performance in tasks involving processing of temporal information both within and across auditory channels. The ability to detect silent gaps within stimuli, regarded as a measure of temporal resolution, has been shown to be generally unaffected by hearing loss especially when differences in stimulus audibility have

FIG. 10. The geometric mean of asynchrony-discrimination thresholds from 10 HI listeners (*filled symbols*) and 6 NH listeners (*open symbols*) from the study by Wojtczak et al. (2012).

been eliminated (Moore et al. 1989, 1992; Schneider et al. 1994; Horwitz et al. 2011). Temporal modulation transfer functions, regarded as another measure of temporal resolution, measured with tonal carriers, also suggest that HI listeners do not exhibit fundamental deficits in temporal processing (Moore and Glasberg 2001). However, deficits due to cochlear hearing loss have been shown in tasks involving comparisons of temporal information across frequency, although not consistently. Across-channel gap detection and gap-duration discrimination measured with frequency-disparate markers preceding and following silent gaps have been shown to be unaffected by hearing loss (Lister et al. 2002; Lister and Roberts 2005). Similarly, the ability to detect a difference in temporal envelope patterns in the presence of an interfering modulation in the remote frequency region is comparable for the NH and HI listeners (Grose and Hall, 1996). On the other hand, CMR known to involve the use of temporally coherent cues across frequency is typically reduced in the presence of hearing loss (Hall et al. 1988; Hall and Grose 1994; Grose and Hall 1996). Because CMR depends on the perceptual grouping of masker and flanking components, Grose and Hall (1996) investigated the possibility that HI listeners may exhibit a faster decline in CMR with increasing onset and offset asynchrony between the masker and flankers than NH listeners. Since comparable changes in CMR with increasing asynchrony were observed in both groups of listeners, Grose and Hall concluded that listeners with cochlear hearing loss do not exhibit deficits in their ability to use gross temporal cues involved in grouping. Similarly, no difference between the NH and HI listeners was observed in that study for the effect of asynchrony between the target and interferer on modulation discrimination interference. However, the effects of across-frequency asynchrony on grouping investigated by Grose and Hall cannot be easily related to the effects of cochlear delays investigated here because the asynchronies that were used to disrupt grouping well exceeded cochlear delays.

In contrast, studies of the intelligibility of tone-vocoded speech have suggested that listeners with cochlear hearing loss do exhibit a reduced ability to integrate temporal information across remote frequency channels (Healy and Bacon 2002; Healy et al. 2005). Not only was the intelligibility score lower for the HI than NH listeners when the speech bands were presented synchronously but also the HI were more sensitive to desynchronizing the bands by 12.5 and 25 ms. Interestingly, not all the HI listeners tested showed the same deficits, suggesting individual differences in the across-channel temporal processing within that group, consistent with the variability of data presented in this study. Healy and Bacon (2002) attributed the differences observed between the NH and HI listeners to a limited ability in the HI to integrate temporal information across frequency channels, but they did not discuss the

possibility that the differences between the two groups may originate from differences in across-frequency cochlear delays. The perceptual consequences of changes to spatiotemporal representations at the output of the cochlea have been mainly studied in the context of processing of within-channel temporal fine-structure information (e.g., Lorenzi et al. 2006; Hopkins and Moore 2011; Moore et al. 2012).

To our knowledge, this study is the first to explicitly examine the effect of cochlear hearing loss on the perception of synchrony across different peripheral channels. The normative data from the NH listeners were collected by Wojtczak et al. (2012) using the same stimuli and procedures. Overall, the data obtained in this study showed variable patterns across individual HI listeners. The variability makes it difficult to provide a generalizable interpretation of the differences between the NH and the HI listeners. In the following sections, specific differences are discussed in relation to the hypothesized higher-level compensation for the frequency-dependent cochlear delays.

Perceived across-frequency synchrony and the cochlear latency–frequency function

For the NH listeners, the maximum proportion of “synchronous” responses in the task involving subjective synchrony judgments corresponded to the pairs of tones that were gated simultaneously. For the HI listeners, the peak of the synchronous-response function was often shifted toward delays corresponding to a pair with a HF-tone leading (Fig. 3). On average, the delay corresponding to the peak was significantly different from 0 ms and was also significantly different from the average peak position estimated for the NH listeners. Under the assumption of higher-level compensation for frequency-dependent cochlear delays, this result is consistent with a “hard-wired” compensating mechanism that did not adapt to the presumed decrease in across-frequency delays produced by hearing loss (Don et al. 1998). However, it should be noted that the shift in the delay corresponding to the maximum synchrony was not observed for all the HI listeners (e.g., HI8 in Fig. 3).

Although the average peak position for the functions measured in experiment 1 was consistent with the hypothesized overcompensation, such an interpretation should be treated with caution. First, based on the published reports, it is not entirely clear that broader filters are associated with substantial changes to the BM latency–frequency function. Cochlear latency–frequency functions estimated from derived-band ABRs and otoacoustic emissions for different levels of the evoking stimuli have been shown to become shallower with increasing level and thus with increasing filter bandwidths (Neely et al. 1988; Schoonhoven et al. 2001; Sisto and Moleti 2007).

However, the validity of those estimates was questioned by Ruggero and Temchin (2007) who argued that such changes in the slope are not supported by physiological animal studies and that they reflect a flawed stimulus design or/and other artifacts of the methods used. Ruggero and Temchin showed that cochlear latency–frequency functions measured in experimental animals *in vivo* and post-mortem differ only slightly in slope and that they become steeper (and not shallower) with the loss of the cochlear active process due to animal's death. According to Ruggero and Temchin, a similar difference should be observed between the human cochlear latency–frequency functions for low-level and for very intense stimuli. Because cochlear hearing loss is associated with broadening of peripheral auditory filters due to the loss of cochlear gain, the effect of hearing loss on the cochlear latency–frequency function should be similar to the effect of a high stimulus level. A recent physiological study by Scheidt et al. (2010) reported that response latencies in the AN of anesthetized chinchillas with noise-induced hearing loss were shorter than those in the normal-hearing animals, but only in fibers that showed broader tuning in addition to threshold elevation after the noise exposure. The decrease in latency was about 0.5 ms, similar to that shown by the postmortem data in the study by Ruggero and Temchin (2007).

Unfortunately, the hearing loss in the study by Scheidt et al. (2010) was induced using a bandpass noise extending from 1 to 4 kHz, and thus, thresholds were elevated over a limited frequency range that did not include CFs below 1 kHz. For humans, the latency–frequency functions estimated from derived-band ABRs measured in the study by Don et al. (1998) suggest that hearing loss in the apical region results in a greater decrease in response latency than that in the basal region of the cochlea. The shift of the peak of the synchronous-response functions measured in experiment 1 can be explained in terms of overcompensation only if the cochlear latency–frequency functions were affected by hearing loss in a way consistent with the effect reported in the study of Don et al..

Another reason for caution in interpreting the data from experiment 1 in terms of changes in relative across-frequency timing of the cochlear responses is that for some of the listeners, the maximum proportion of “synchronous” responses was only around 0.5 (e.g., HI1, HI2, HI3). This result could suggest that some HI listeners had very low confidence in the “synchronous” judgment or that they had a strong bias towards choosing the “asynchronous” response. Since it is not clear why HI listeners should be more biased than the NH listeners toward the “asynchronous” response, the explanation in terms of uncer-

tainty about the decision appears more likely. Although the correlation shown in Figure 5B did not reveal a systematic relationship between the peak of the synchronous-response functions and listeners' age, some of the differences between the data from the NH and HI listeners may reflect a degraded coding of timing information due to aging and not due to the cochlear hearing loss *per se* (Fitzgibbons et al. 2007; Parthasarathy and Bartlett 2011).

Asynchrony detection and the slopes of the synchronous-response functions

In NH listeners, asynchrony-detection thresholds and thresholds for detecting an increase in asynchrony for small baseline asynchronies have been found to be lower for tone pairs with the LF-tone leading than for pairs with the HF-tone leading (Wojtczak et al., 2012). The dependence of thresholds on the frequency order was consistent with the asymmetry of the synchronous-response functions in the same listeners, which showed a greater decrease in the proportion of “synchronous” responses with increasing delay between the tones (i.e., a steeper slope) for the pairs with the LF- than HF-tone leading. In the current study, the synchronous-response functions from the HI listeners were variable with respect to the pattern of asymmetry (see Fig. 6), not only across listeners (e.g., HI3 versus HI8) but also across the frequency pairs for a given listener (e.g., HI2). For listeners whose data exhibited steeper slopes on the side above the peak of the synchronous-response function, asynchrony-detection thresholds were generally lower for the HF-lead condition in experiment 2, indicating that the results from the two experiments were qualitatively equivalent. However, for the listeners with the asymmetry pattern similar to that observed for the NH listeners (i.e., with a steeper slope below the peak), even qualitative correspondence between results from the two experiments was poor. For example, although asynchrony-detection thresholds were consistently lower in the LF- than the HF-lead condition for listener HI4, listener HI5 showed a reversed threshold pattern, despite the fact that the two listeners had similar shapes of the synchronous-response functions. Synchronous-response functions for three of the listeners (HI6, HI7, and HI9) exhibited a plateau on one side over the range of delays used in experiment 1. Despite no change in the slope, listeners HI6 and HI7 had relatively low asynchrony-detection thresholds measured in the 3AFC task. It is possible that visual feedback helped them find a cue that they missed when performing subjective judgments without feedback. Listener HI9, on the other hand, had surprisingly high asynchrony-detection thresholds in the LF-lead condition, given a

near-normal slope of the synchronous-response function on the side corresponding to pairs with the LF-tone leading. We have no clear explanation for these anomalous results. Overall, the inconsistencies between the data from the two experiments likely reflect different strategies and/or cues used in the two tasks, resulting in poor agreement between the model predictions and the data (Fig. 9).

Age versus hearing loss

The aim of this paper was to evaluate the effect of hearing loss on the perception of across-frequency timing information. However, the HI listeners in this study were on average older than the NH listeners in the study by Wojtczak et al. (2012) used as a control group. A large number of studies have reported clear effects of age on gap detection and gap-duration discrimination for both within-channel and across-channel markers (Fitzgibbons and Gordon-Salant 1994; Schneider et al. 1994; He et al. 1999; Lister et al. 2000, 2002; Lister and Roberts 2005). Since the NH and HI listeners compared in this study were not age-matched, some of the observed differences between their data may reflect poorer coding of temporal information or a reduced ability to integrate temporal information across frequency due to the age of the HI listeners. In experiment 1, the maximum proportion of synchronous responses was often low, perhaps indicating some difficulty in making judgments about synchrony across frequency. The mean results from experiment 2 (Fig. 10) showed generally higher thresholds in the asynchrony-discrimination task for the (older) HI than the (younger) NH listeners. However, performance in neither experiment was significantly correlated with listeners' age. The lack of significant effects of age may be at least partly associated with the use of pure tones as test stimuli. Age effects in within- and across-frequency gap-detection tasks have been shown to diminish for pure-tone markers compared with more complex noise or speech markers (e.g., Lister and Roberts 2005; cf. Heinrich and Schneider 2006). The age dependence of the ability to detect silent gaps has also been shown to disappear at a relatively long (500 ms) duration of pure-tone markers (Schneider and Hamstra 1999). However, a clear separation of the effect of age versus hearing loss on performance in the two experiments within this study would require that the two groups of listeners be age-matched for investigating the effects of hearing loss and matched with respect to hearing loss when investigating the effects of age. The fact that age and hearing loss of the listeners were significantly correlated in this study complicates the interpretation in terms of either effect alone.

Whether the differences in the processing of across-frequency timing information between the two groups shown in this study were due to age or

hearing loss or both, it is clear that these differences vary across the hearing-impaired individuals. This outcome implies that algorithms that simply mimic the normal cochlear latency–frequency function are not sufficient for bringing the across-frequency timing in HI listeners back to normal alignment. Thus, given the data presented here, it should not be surprising that algorithms attempting to implement such corrections have not been generally successful at improving speech intelligibility (Shi et al. 2006; Calandruccio et al. 2007).

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