Peripheral auditory processing, the precedence effect and responses of single-units in the inferior colliculus

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ABSTRACT

The purpose of this report is to show how monaural, peripheral, auditory processing may affect binaural performance in "precedence" experiments employing successive pairs of binaural transients. Interactions within peripheral auditory filters are shown to result in internal, effective interaural delays and interaural intensitive differences that differ from those within the external stimuli.   Such peripheral interactions, when combined with hair-cell adaptation and compression, are manifested via binaural cross-correlation. The across-frequency average of the cross-correlation accounts for classic data obtained in precedence experiments employing transient or "short" stimuli separated by times short enough to produce only one intracranial image.

Introduction

We have recently described how monaural, peripheral, auditory processing may explain behavioral data obtained in binaural "precedence" experiments in which interaural temporal differences (ITDs) are conveyed by successive pairs of binaural transients (Hartung and Trahiotis, 2001). We showed that combining filter interactions, hair-cell based compression and adaptation (Meddis, 1986, 1988; Meddis et al. 1990) and binaural cross-correlation could account for the forms of the data obtained in experiments reported by Wallach *et al.*(1949), Yost and Soderquist (1984), Shinn-Cunningham *et al.* (1995). More specifically, when the time between the pairs of transients within a single ear is below two to three ms relevant interactions can occur within peripheral auditory filters. For the interactions to occur, the time between the monaural inputs has to be effectively shorter than the reciprocal of the bandwidth of the auditory filter being stimulated (see Jeffress and McFadden, 1968).

The purpose of this paper is to discuss those outcomes and to illustrate how such interactions within peripheral auditory filters are relevant to the interpretation of certain data obtained in recent physiological studies seeking to find physiological correlates of behavioral precedence-effect phenomena (e.g. Yin, 1994; Fitzpatrick *et al.*, 1995; Litovsky and Yin*.,* 1998). The physiological data of interest are responses from single neural units in the inferior colliculus recorded following stimulation by successive pairs of binaural clicks. It is typically found in such studies that neural units which are "tuned" to particular values of ITD show severely diminished responses to these "best-ITDs" when they are first stimulated by another pair of binaural transients conveying an ITD to which the neurons do not respond vigorously (what Fitzpatrick *et al.* term the "worst/best" case).

It is shown that the diminished responses obtained when the ITDs are presented in the "worst/best" configuration with short interclick-intervals can be understood by considering peripheral auditory filtering. Auditory filtering produces internal values of ITDs and IIDs that can differ greatly from those within the external stimulus and even be "outside the ITD tuning range" of a single unit being studied.

In order to understand how within-filter interactions occur, consider that the duration of the impulse response of a filter is inversely related to the filter's bandwidth. The duration of the impulse response (or total "ringing"-time) of auditory filters centered between 250 Hz and 1 kHz is in the range of 20 to 30 ms, or so. Therefore, the impulse responses of two successive inputs for such low-frequency filters will, at least partially, overlap when the inputs are separated by less than 20 ms or so. Because the time interval between successive clicks in precedence-like experiments is typically in the range of about 1 to 4 ms, within filter interactions must occur. Such within filter interactions are well known but, to our knowledge, until now have not been shown to produce changes in the values of ITDs and IIDs conveyed by the two monaural inputs.

Figures 1 and 2 illustrate binaural consequences of monaural within-filter interactions for pairs of 100 μs-long clicks such as those presented by Fitzpatrick et al. (1995) in what they termed a "worst/best" configurations (see their Figure 5C). By worst/best, it was meant that the ITD applied to the first member of a pair of binaural clicks was a value that elicited the smallest or no neural response while the ITD applied to the second member of the pair of binaural clicks was the value determined to produce the most vigorous response for binaural clicks presented in isolation. In our example, the ITD imposed on by the first pair of binaural clicks is 0 μs and the ITD imposed on the second pair is -600 μs, indicating a 600 μs lead to the right ear. The inter-click interval (ICI) is 2 ms for the leftmost column, 4 ms for the center column and 8 ms for the rightmost column. This range of ICIs is highly relevant for interpretation of physiological correlates of many precedence-related phenomena, including the echo threshold (Blauert, 1997).
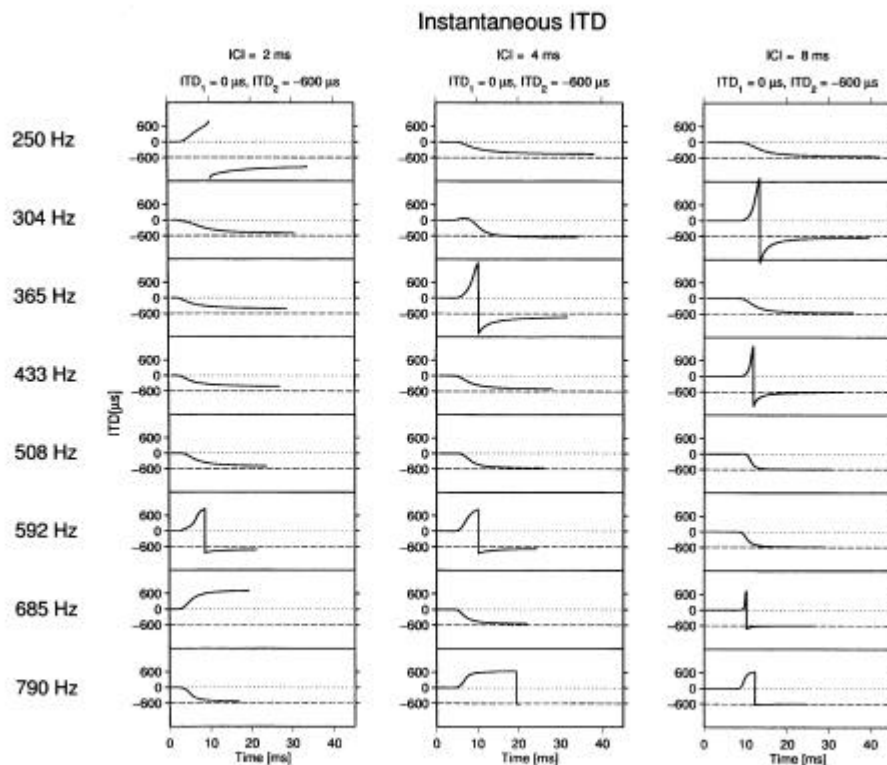

Figure 1

Within each column are shown instantaneous ITDs (Fig. 1) and IIDs (Fig. 2) obtained by comparing the left/right outputs from gammatone filters having center frequencies between 250 Hz and 790 Hz and spaced in one ERB intervals (Glasberg and Moore, 1990). For reference, the external values of ITD for the first pair of clicks (ITD_1) are indicated by the dashed lines and those for the second pair of clicks (ITD_2) are indicated by the dotted lines. The ITDs and IIDs were obtained from the analytic signals that resulted from the application of the filter. ITDs were indirectly obtained via interaural phase differences ($\Delta\Phi$) which were derived from the scalar products and vector products of the left and right analytic signals. The interaural phase differences were then transformed into ITDs by taking into account the center frequency of the auditory filter. The values of IID (Fig. 2) are expressed in dB as 20 times the logarithm of the ratio of the left and right envelope-functions.

Beginning with the leftmost column of Figure 1 when the ICI was 2 ms, note that the ITDs change over time and are very different from those present in the inputs. For example the outputs of the left/right filters centered at 250 Hz initially convey ITDs of 0 µs, like the input. They then convey "internal" ITDs that differ markedly from that within the physical stimulus. The internal ITDs first indicate that the left ear leads by more than 600 µs! This is followed by an abrupt switch to internal ITDs of more than –600 µs, indicating that the right ear is leading! Clearly, the within filter interaction have dramatically altered the ITDs present at the input. Visual inspection of the ITDs conveyed by the other filters also indicates internal values of ITD that are unlike those imposed on the physical stimuli and which differ from one filter to another.

For our example, it is important to understand what would pertain if the outputs of any of these filters were to provide input to cells in the inferior colliculus which were "best-tuned" to an ITD of –600 µs. Figure 1 suggests that the response of the neuron would be weak or absent until more than 10 ms after the clicks were presented simply because the ITDs at the outputs of each of the filters would convey ITDs to which the unit would not be expected to respond. In addition, the figure indicated that one could not predict accurately the strength of the neural responses thereafter without knowing which filter(s) provide inputs to the cell. The output of the filter centered at 685 Hz provides an apt example. Were the output of that filter to serve as the sole input to our hypothetical cell, then one would expect no responses to the stimulus because the output of that filter never shows ITDs near –600 µs.

A similar complex patterning of ITDs that differs across filters of different center frequencies is seen when the ICI is 4 ms (middle column). Although the detailed nature of the ITDs differs over time and across filters from when the ICI was 2 ms, once again ITDs of other than –600 us to which the neuron is tuned are evident. Consequently, even for this larger ICI, one would expect greatly diminished neural responses.

Note, however, that when the ICI is extended to 8 ms, three "ITD states" occur. During the first 8 ms or so the ITDs are 0 µs, mimicking the ITD conveyed by the first pair of clicks. Then over the next several milliseconds there occur complexly patterned transitional values of ITD which are followed by ITDs of approximately –600 µs. The third state shows no effect resulting from within-filter interaction. The "final" ITD is the ITD conveyed by the second pair of clicks and the ITD to which our hypothetical neuron responds "best".

Figure 2 contains instantaneous IIDs measured for the same stimuli. Note that complex and divergent patterns of IID are evident in the outputs of the bank of left/right filters for each of the three values of ICI. Rather than dwelling on details suffice it to say that filtering has produced several occurrences of instantaneous IID having magnitudes of 10 or 30 dB or so even though the IID conveyed by the external stimuli is 0 dB. Taken together, the information in Figures 1 and 2 strongly suggest that one would require detailed knowledge concerning the spectral regions that provide input to the neural units under study in order to interpret their responses to compound stimuli.
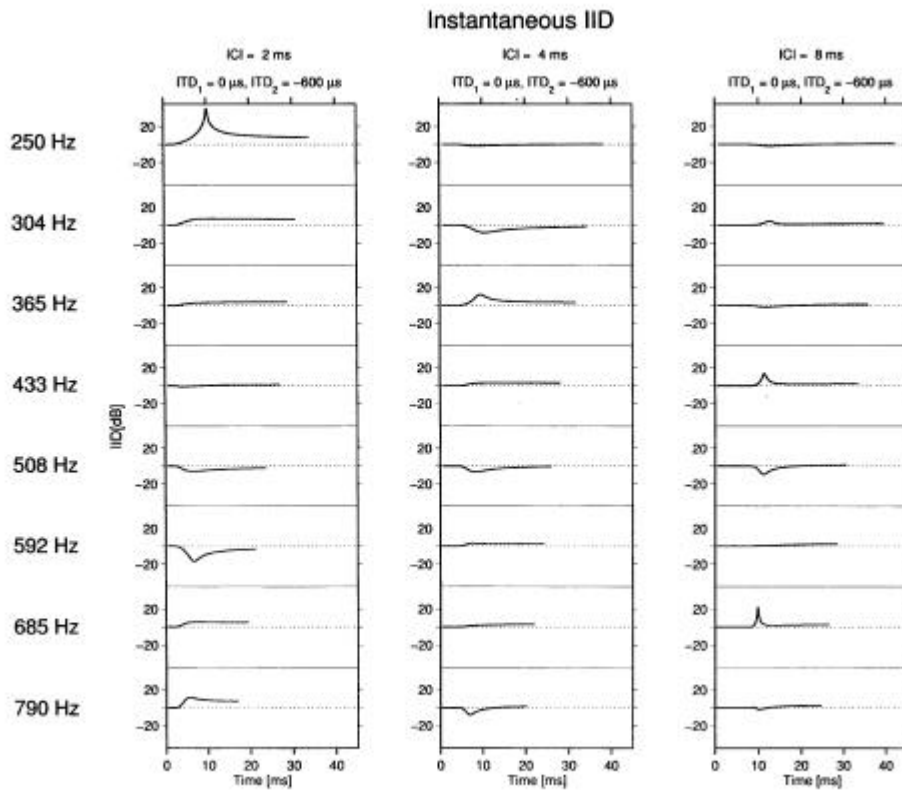
Instantaneous IID

Figure 2

Conclusion

Monaural peripheral auditory processing produces values of dynamically changing binaural cues that may not reflect those imposed on the physical stimuli. This is a natural consequence of auditory filtering and peripheral compression and adaptation. Taking into account such interactions appears necessary for the proper interpretation of physiological data obtained from single neural units in precedence-like experiments. In addition, the effects produced by peripheral filtering and compression and adaptation should either be eliminated or explicitly recognized before mechanisms such as "central inhibition" or "echo suppression" are invoked as explanations of neural data.

Acknowledgments

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