Variations on a Dexterous theme: Peripheral time–intensity trading

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Abstract

Sound pressure level changes can affect the timing of spiketrains. Timing of spiketrains is critical for sensitivity to interaural timing differences (ITDs). Interaural level differences (ILDs) can therefore affect the ITD cue. It has been hypothesized that ILDs may be coded indirectly through a peripheral conversion of level to time (but it should be cautioned that the changes in phase with SPL in low-CF AN fibers of the cat are more complicated) (Jeffress, L.A., 1948. A place theory of sound localization. J. Comp. Physiol. Psychol. 41, 35–39). We tested this conversion by recording from auditory nerve fibers to broadband noise at different SPLs. For each fiber, correlograms were constructed to compare timing to fine-structure across SPLs. We find generally a decrease in the time delay between spikes and the stimulus with increasing SPL. However, the magnitudes of the shift in time are surprisingly small, and dependent on characteristic frequency (CF): the largest shifts are approximately 10 μs/dB and occur at the lowest CFs. Nevertheless, the effects of level on spike timing are systematic and of a magnitude to which the binaural system is sensitive. Thus, even though the results indicate that ILD is not traded for ITD in a simple way, the possibility that low-frequency ILDs affect the binaural percept via a peripheral level-to-time conversion cannot be excluded.

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1. Introduction

The "latency hypothesis" refers to the idea that sensitivity to interaural level differences (ILDs) arises through a peripheral conversion of sound level to latency of neural response, and that these latency shifts are subsequently detected by the neural mechanisms subserving the processing of interaural time differences (ITDs). The hypothesis was most famously put forward in a single paragraph of Jeffress' celebrated paper (Jeffress, 1948), at a time when physiological knowledge of the auditory periphery was based on compound potentials. It was inspired by the psy-

chophysical phenomenon of "time–intensity trading" which shows that ILDs and ITDs can interact (Green and Henning, 1969; Moushegian and Jeffress, 1959), and the observation that the compound action potential shows a decrease in latency in the order of milliseconds with increasing SPL (review in Eggermont, 1976).

Dexter Irvine and colleagues tested the latency hypothesis in the lateral superior olive (LSO) with a particularly elegant paradigm. They found that, for some neurons, ITD- and ILD-sensitivity could be mapped onto each other using SPL-induced changes in latency measured on the same neurons (Irvine et al., 2001). Importantly, their study, as well as other preceding physiological studies that specifically addressed the latency hypothesis, focused on transient responses at high frequencies (Hirsch et al., 1985; Irvine et al., 1995, 2001; Park et al., 1996; Pollak, 1988; Yin et al., 1985), while Jeffress' hypothesis was concerned with sensitivity to ongoing ITDs and ILDs at low frequencies.

Oddly, while the latency hypothesis is popular with physiologists, it no longer is with psychophysicists. This

situation seems to arise partly from the difference in emphasis just mentioned. Physiologically, it is important to distinguish three categories of temporal locking: to a waveform's onset, its fine-structure, and its envelope. There is ample evidence that the onset latency of auditory neural responses generally decreases with SPL. The decrease is typically on a millisecond time scale (Kiang et al., 1965; Kitzes et al., 1978), and is therefore large relative to the ITDs to which the binaural system is sensitive. Thus, in circumstances in which the onset response is important, ILD may indeed affect the magnitude of the peripheral neural representation of ITD, henceforth referred to as the "internal ITD" (see below). However, for sustained responses that are temporally locked to sustained stimuli, the effect of SPL is more complex. Early studies of the auditory nerve (AN) already showed that the phase of responses that are phase-locked to the ongoing fine-structure of low-frequency tones is rather stable as a function of intensity when the stimulus frequency equals the fiber's characteristic frequency (CF: frequency of lowest threshold)(Rose et al., 1967). For other frequencies, the extent and direction of the effect of SPL depends on the relationship of the tone's frequency to the fiber's CF, as shown in the classical study of Anderson et al. in the AN of the squirrel monkey (Anderson et al., 1971). For tones away from CF, increasing SPL causes a progressive phase lag (at frequencies below CF) or lead (at frequencies above CF). The relatively simple picture that emerged from the study of Anderson et al. is consistent with measurements of basilar membrane vibration at the cochlear base (reviewed by Robles and Ruggero (2001)) and is generally thought to reflect the compressive nonlinearity of the inner ear (but it should be cautioned that the changes in phase with SPL in low-CF AN fibers of the cat are more complicated: Allen, 1983; van der Heijden and Joris, 2006b). Thus, in response to pure tones, the timing of the response of AN fibers to stimulus onset behaves quantitatively and qualitatively different from the timing of the ongoing response. Similar observations have been made for most cell types in the cochlear nucleus (Kitzes et al., 1978; Lavine, 1971), as well as for ongoing temporal responses to the stimulus envelope (Joris et al., 2004; Møller, 1975).

What is known regarding the interaction of level and time in binaural neurons? While an ILD–ITD interaction is well-established for onset responses of binaural neurons and is relatively straightforward (Hirsch et al., 1985; Irvine et al., 1995, 2001; Park et al., 1996; Pollak, 1988; Yin et al., 1985), the situation is again more complex for ongoing responses. The effect of combinations of ILDs and ITDs on ongoing responses of binaural neurons has been studied both to low-frequency pure tones (Finlayson and Caspary, 1991; Goldberg and Brown, 1969; Joris and Yin, 1995; Kuwada and Yin, 1983; Palmer et al., 2007; Tollin and Yin, 2005; Viete et al., 1997; Yin and Kuwada, 1983; Yin and Chan, 1990) and to high-frequency amplitude-modulated tones (Batra et al., 1993; Joris and Yin, 1995). Clearly, even for sustained stimuli, ILDs and ITDs can interact at the single neuron level in the sense of jointly affecting the output rate of binaural neurons. In many instances such cue interaction reflects a central mechanism (e.g. inhibition in the LSO) rather than a peripheral level-to-time conversion. We will concern ourselves here only with instances where the main effect of ILD is a phase shift of the low-frequency binaural response (Kuwada and Yin, 1983; Palmer et al., 2007; Viete et al., 1997; Yin and Kuwada, 1983).

In these reports, the binaural phase shifts were indeed interpreted as the reflection of a peripheral level-to-time conversion, but not necessarily of a kind consistent with the "simple" decrease in onset latency with SPL (i.e. as it occurs in the timing of the onset response). It is in fact unclear whether the mechanisms causing "simple" decreases in latency play any role at all in sustained binaural responses. Rather, the binaural shifts observed are reminiscent of the complex change in the cochlear transfer function with SPL already mentioned (Anderson et al., 1971; Robles and Ruggero, 2001). In a large sample of IC neurons (Yin and Kuwada, 1983), about two-thirds of the neurons studied showed binaural phase shifts in a direction opposite to that expected from a simple decrease in latency with SPL, and this seemed to be independent of stimulus frequency. An increasing phase lag with increasing SPL was also the predominant result in binaural neurons of the nucleus laminaris of the barn owl (Viete et al., 1997), but the slope of the phase shift depended on the relationship of frequency to CF and was largely consistent with phase shifts at the peripheral monaural level (Koppl, 1997; Viete et al., 1997), which in turn were similar to the shifts reported in the mammalian AN by Anderson et al. (1971). In contrast, in the IC of the guinea pig, Palmer et al. (2007) found predominantly decreasing phase lags with increasing SPLs (i.e. phase shifts consistent with a decrease in latency with SPL), but in some neurons both decreasing and increasing phase shifts were observed in a frequency-dependent pattern broadly reminiscent of the data of Anderson et al. (1971). In summary, most binaural data to sustained tones show level effects which run counter to the latency hypothesis, but the effects are variable across neurons and across studies.

Our interest and approach differ from previous studies in a number of respects. First, the latency hypothesis proposes a peripheral conversion of intensity to time. It can therefore be tested most directly at a peripheral level. We are mainly interested in effects on fine-structure and therefore choose to study AN fibers with low CF. Second, we studied responses to broadband Gaussian noise, which is a generic stimulus often used in binaural psychophysical studies, rather than to pure tones. As mentioned, previous AN studies with pure tones show a relatively complex pattern of phase changes with SPL (Allen, 1983; Anderson et al., 1971). This makes it difficult to predict the overall effect, across the AN array, of SPL on the timing of responses to tones and particularly to broadband stimuli. To obtain such an overview, we recorded from many AN