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Research Report

The temporal representation of the delay of dynamic iterated rippled noise with positive and negative gain by single units in the ventral cochlear nucleus

*Mark Sayles, Ian Michael Winter**

Centre for the Neural Basis of Hearing, The Physiological Laboratory, Downing Street, Cambridge, CB2 3EG, UK

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ABSTRACT

Spike trains were recorded from single units in the ventral cochlear nucleus of the anaesthetised guinea-pig in response to dynamic iterated rippled noise with positive and negative gain. The short-term running waveform autocorrelation functions of these stimuli show peaks at integer multiples of the time-varying delay when the gain is +1, and troughs at odd-integer multiples and peaks at even-integer multiples of the time-varying delay when the gain is −1. In contrast, the short-term autocorrelation of the Hilbert envelope shows peaks at integer multiples of the time-varying delay for both positive and negative gain stimuli. A running short-term all-order interspike interval analysis demonstrates the ability of single units to represent the modulated pitch contour in their short-term interval statistics. For units with low best frequency ($\lesssim$1.1 kHz) the temporal discharge pattern reflected the waveform fine structure regardless of unit classification (Primary-like, Chopper). For higher best frequency units the pattern of response varied according to unit type. Chopper units with best frequency $\gtrsim$1.1 kHz responded to envelope modulation; showing no difference between their response to stimuli with positive and negative gain. Primary-like units with best frequencies in the range 1–3 kHz were still able to represent the difference in the temporal fine structure between dynamic rippled noise with positive and negative gain. No unit with a best frequency above 3 kHz showed a response to the temporal fine structure. Chopper units in this high frequency group showed significantly greater representation of envelope modulation relative to primary-like units with the same range of best frequencies. These results show that at the level of the cochlear nucleus there exists sufficient information in the time domain to represent the time-varying pitch associated with dynamic iterated rippled noise.

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* *Corresponding author.*
E-mail address: imw1001@cam.ac.uk (I.M. Winter).

Abbreviations: ACF, autocorrelation function; ANF, auditory nerve fibre; BF, best frequency; CN, cochlear nucleus; CS, sustained chopper; CT, transient chopper; CV, coefficient of variation; DIRN, dynamic iterated rippled noise; FM, frequency modulation; IRN, iterated rippled noise; ISIH, interspike interval histogram; LF, low frequency unit; PL, primary-like; PN, primary-like with notch; PSTH, peri-stimulus time histogram; VCN, ventral cochlear nucleus

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1. Introduction

1.1. IRN signals and perception

Pitch is an important aspect of our everyday auditory sensation. For example, differences in pitch are a major cue for the perceptual segregation of sound sources, whereas sounds with similar pitches tend to be grouped into auditory objects. Neurophysiological and psychophysical studies of pitch perception have commonly used stimuli with static pitches although it is well known that speech sounds contain modulated pitch contours on multiple time scales (e.g. O'Shaughnessy and Allen, 1983). These include formant and fundamental frequency transitions characteristic of consonants (Liberman et al., 1956) and transitions on longer time scales providing prosodic information (*cf.* Poeppel, 2003). In some languages changes in pitch can even provide lexical distinction (Stagray et al., 1992). Here we examine the neurophysiological representation of dynamic pitch by utilizing a stimulus, iterated rippled noise (IRN), which has been extensively used to study the representation of static pitch in the nervous system (see below). Rippled noise is produced by passing a broadband signal such as white noise through a delay-and-add filter. The output signal contains peaks in the amplitude spectrum and elicits the sensation of a pitch at the delay, *d*, known as repetition pitch (Bilsen and Ritsma, 1969/70). This effect occurs in our natural environment and was first described by the Dutch physicist Christian Huygens in 1693. In this early demonstration the effect was produced by the interaction of a source of broadband noise (falling water from a fountain) and a nearby reflective surface (a stone staircase). Standing between the fountain and staircase Huygens noticed the emergent pitch, and attributed this to the iterative delay and add process introduced by the series of regularly spaced steps. A similar process can be implemented using digital signal processing to delay a broadband noise by time *d*, multiply it by a gain factor *g* and add it back to the original waveform. By iterating the delay and add process the pitch strength increases (Yost et al., 1996), and the resulting signal is known as iterated rippled noise. The iterative delay and add process introduces temporal regularity into the fine structure of the noise and a "ripple" into the long-term power spectrum of the waveform. When the gain factor *g* is positive (IRN(+)) the perceived pitch corresponds to 1/*d* Hz. When the gain is negative (IRN(−)) the perceived pitch depends on the stimulus frequency content and number of iterations. For broadband IRN(−) with high iteration number (>4) the perceived pitch corresponds to 1/2*d* Hz (Raatgever and Bilsen, 1992; Yost, 1996). The perceived pitch of band-filtered IRN(−), and broadband IRN(−) with less than 4 iterations (Yost, 1996) is ambiguous; with subjects matching the pitch to values corresponding to 0.88/*d* Hz, 1.14/*d* Hz and 1/2*d* Hz (Bilsen and Ritsma, 1969/70; Raatgever and Bilsen, 1992). The difference in pitch between IRN(+) and IRN(−) reflects a difference in the temporal fine structure of the stimuli, which can be demonstrated by comparing their waveform autocorrelation functions (ACFs). The waveform ACF for IRN(+) shows peaks at *d* and its integer multiples, whereas for broadband IRN(−) there are troughs at *d* and its odd-integer multiples with peaks at even-integer multiples of *d*. In contrast, the ACFs of the signal envelopes of IRN(+) and IRN(−) both contain peaks at *d* and integer multiples thereof (Yost et al., 1998; Shofner, 1999; see Fig. 1). The temporal fine structure of a waveform refers to the rapid variations in pressure, whereas the waveform temporal envelope refers to the slower changes in amplitude of these rapid pressure fluctuations. The envelope of the broadband waveform can be extracted in several different ways. The simplest is to apply half-wave rectification and low-pass filtering to the signal, whereas the "true" envelope in a mathematical sense is the Hilbert envelope, which is the magnitude of the analytic signal (see Hartmann, 1997).

At relatively low frequencies (below approximately 3 kHz in the guinea pig) auditory nerve fibres (ANFs) can represent the temporal fine structure information in their phase-locked discharge patterns. At higher best frequencies, beyond the limit of phase-locking, the temporal discharge pattern reflects the envelope modulation at the output of the peripheral filter. Using band-filtered IRN in psychophysical experiments several authors have demonstrated a change in the perceived pitch of IRN(−) from 1/2*d* Hz (corresponding to the temporal fine structure) to 1/*d* Hz (corresponding to the envelope periodicity) as the filter centre frequency is increased (Wiegrebe and Winter, 2001b; Yost et al., 1998; Supin et al., 1994).

In the environment the effects of the delay and add process are particularly salient when the broadband source is in motion, so that the delay between the direct and reflected sounds changes as a function of time, resulting in a modulated pitch sensation. For example the sound of a jet airplane and the reflections of this broadband noise from nearby buildings results in a filtered signal with a moving delay as the airplane takes off (Hartmann, 1997). Bilsen and Ritsma (1969/70) describe a similar situation involving a steam train blowing off steam whilst stationary at a platform. Standing on the platform the listener hears a repetition pitch due to reflected sound from the station platform adding back (after some delay) with the original broadband noise from the steam at the listener's ears. As they walk towards the locomotive the listener hears the pitch becoming progressively lower. Both of these examples involve the introduction of a time delay between the arrival of the direct and indirect components of sound at the ears which itself varies as a function of time. If the travel-time (and hence the time delay, *d*) between a series of steps was not constant, but monotonically increasing or decreasing with step number, we might also predict a modulated repetition pitch. Such architecture has been suggested as the origin of the chirped-echo effect noticed at the ancient Mayan stone pyramid at Chichen Itza in Mexico (Lubman, 1998; Declercq et al., 2004). In response to a handclap (or presumably any other broadband impulsive sound) the listener, standing at the foot of the pyramid, hears an echo containing a frequency glide, which has recently been explained as a repetition pitch (Bilsen, 2006) in which the repetition period grows gradually longer. Bilsen (2006) notes that at the pyramid a continuous sound source such as broadband noise would not elicit the same frequency glide percept due to the simultaneous mixing of all the different delays. It is possible though with digital techniques, by making the delay itself a function of time, to create IRN with a non-static pitch; this has been termed dynamic iterated rippled noise (DIRN) (Denham,

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