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Research paper

The temporal representation of the delay of iterated rippled noise with positive or negative gain by chopper units in the cochlear nucleus

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Abstract

The role of chopper units in representing the pitch of complex sounds is unresolved. Traditionally chopper units have been regarded as primarily responding to the stimulus envelope of complex stimuli. This has been supported by the response of chopper units to iterated rippled noise (IRN) as they can provide a robust representation of the delay of IRN with positive gain (+) in their first-order interspike intervals and for some chopper units this representation is relatively level independent. The envelope modulation of IRN(+), and pitch, is at the reciprocal of the delay, the pitch of IRN with negative gain (IRN(−)) is often at twice the delay. This distinction between IRN(+) and IRN(−) can be used to help determine whether a unit is simply responding to modulation or to stimulus fine structure. Chopper units with relatively high best frequencies (BF) are unable to represent the distinction between IRN(+) and IRN(−). However, in this study it is shown that at least some chopper units, with low BFs (<1.25 kHz), can represent the pitch of the IRN(−) as perceived perceptually.

Keywords: Multi-polar cell; Pitch; Inter-spike intervals; Autocorrelation

1. Introduction

Although an oversimplification there are essentially two competing theories for the neural representation of the pitch of complex sounds; place and temporal. Place theories rely on the frequency resolving properties of the basilar membrane while temporal theories rely on the temporal properties of the discharge patterns of auditory nerve fibres. Both theories suffer from a lack of knowledge about how a neural implementation is achieved at higher levels of the auditory pathway. For place theories it is commonly assumed that there must be a harmonic template that allows comparison of the input with previously stored templates but evidence for this is lacking. In contrast, temporal theories, often represented by all-order interspike intervals (akin to the autocorrelation), require a neural mechanism to perform an autocorrelation over durations of at least 30 ms; evidence for such a time constant is also lacking. However, one way of implementing a neural representation of pitch using temporal information is to use a series of band-pass periodicity filters and these have been described at both the level of the Cochlear Nucleus (CN: Frisina et al., 1990a,b; Kim et al., 1990; Rhode and Greenberg, 1994; Wiegrebe and Winter, 2001a) and the Inferior Colliculus (IC: Langner, 1981; Langner and Schreiner, 1988). In the CN these cells are often, but not exclusively, characterized by 'chopper' discharge patterns in response to suprathreshold best-frequency (BF) tone bursts but the role

Abbreviations: BF, best frequency; CN, cochlear nucleus; CS, sustained chopper; CT, transient chopper; CV, coefficient of variation; CW, wide-mode chopper; DCN, dorsal cochlear nucleus; IC, inferior colliculus; IRN, iterated rippled noise; ISIH, interspike interval histogram; PL, primary-like; PSTH, post-stimulus time histogram; VCN, ventral cochlear nucleus; WN, white noise

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of chopper units in the temporal representation of the pitch of complex sounds is controversial. This controversy has been partly fuelled by recent studies using iterated rippled noise (IRN) to investigate the representation of pitch by single units in the cochlear nucleus using either first-order and all-order inter-spike intervals (Shofner, 1991, 1999; Winter et al., 2001; Wiegrebe and Winter, 2001a,b).

IRN is produced by repeatedly delaying a random noise by a delay (d), multiplying it by a gain and adding it back to the original. The delay-and-add process introduces temporal regularity into the fine structure of the noise as well as a 'ripple' into the long-term power spectrum of the wave (e.g. Yost, 1996a; Yost et al., 1996). The peaks in the amplitude spectrum depend on the gain. The peaks are at multiples of $1/d$ Hz for IRN with a gain of 1 (IRN(+)) and at $1/(2d)$ Hz and its odd-integer multiples for IRN with a gain of −1 (IRN(−)). For IRN(+) the perceived pitch is always equal to the reciprocal of the delay and for the broadband IRN(−) stimulus used in the present study (with 16 iterations) the perceived pitch is equal to $1/(2d)$. The autocorrelation function of IRN(+) has peaks at the delay and its integer multiples. The autocorrelation function of IRN(−) has nulls corresponding to the delay and odd-integer multiples of the delay, and positive peaks at even-integer multiples of the delay. The largest peak in the autocorrelation function of the waveforms of the two IRN corresponds to their perceived pitch. In contrast to the differences between the autocorrelation functions of the stimulus waveform, the autocorrelation functions of the stimulus envelope are virtually identical for IRN(+) and IRN(−). Thus, the pitch difference between IRN(−) and IRN(+) is determined by differences in the fine-structure and not in the envelope of the waveform. In human psychophysical experiments the perceived pitch of *highpass-filtered* IRN(−) depends on the cutoff frequency of the highpass filter and the delay of the IRN. For example, listeners switch from hearing an octave shift between IRN(−) and IRN(+) with the same delay of 4 ms to hearing the same pitch for the two IRN stimuli when the cut-off was raised from 1250 to 2500 Hz. The switch occurs at higher frequencies for shorter delays (Wiegrebe and Winter, 2001b) These psychophysical results have to be kept in mind when chopper units are judged as to whether they are suitable to code the pitch-deviations between IRN with positive and negative gain.

Previous studies have demonstrated that the predominant interval in an autocorrelation analysis of populations of auditory nerve fibres provides a robust representation of the pitch for a wide variety of complex sounds (Cariani and Delgutte, 1996a,b). This finding has been extended to the use of IRN in both the auditory nerve and ventral cochlear nucleus (VCN) (ten Kate and van Bekkum, 1988; Shofner, 1991, 1999; Winter et al., 2001; Wiegrebe and Winter, 2001a), where it was shown that the delay of IRN is represented in the first- and all-order inter-spike interval histograms (ISIHs). Using infinitely iterated rippled noise (IIRN), Shofner (1999) showed that the majority of phase-locking primary-like (PL) units had peaks in their neural autocorrelograms at integer multiples of the delay when the gain was +1 but nulls flanked by a pair of positive peaks at d and odd-integer multiples of d when the gain was −1. Chopper units on the other hand mostly showed peaks at multiples of the delay irrespective of the gain. Given that IIRN with positive and negative gain has the same envelope autocorrelation function, Shofner (1999) concluded that some PL units encode the waveform fine-structure of the stimulus whereas chopper units represent features of the stimulus envelope. In a study on the VCN of the guinea pig, Winter et al. (2001) showed that the delay of IRN(+) is not only represented as peaks in the all-order ISIHs, but the units, including choppers, were also tuned to certain IRN-periodicities as estimated by their first-order ISIHs. The bandpass periodicity preference of some sustained chopper (CS) units was found to be level-independent leading Wiegrebe and Winter (2001a,b) to propose that chopper units may be important in representing the pitch of complex sounds to higher centres. This was in contrast to the results of Shofner (1991, 1999) who emphasized the role of primary-like units in the representation of the delay of IRN(+) and IRN(−). Unfortunately, Winter and colleagues did not investigate the responses of chopper units to IRN(−) and therefore the aim of this study was to extend the findings of Shofner (1999) and Winter et al. (2001) by comparing the responses of chopper units with low BFs to IRN(+) and IRN(−). Here we show that some chopper units (6/12), with BFs less than 1.1 kHz, show a clear difference in their response to IRN(−) and IRN(+), with a local minimum in their ISIH at the delay d and a peak at $2d$ for IRN(−) and a peak a 'd' for IRN(+), i.e. these units show a response to the stimulus fine structure. In order to investigate if the units are able to represent the pitch of IRN the units have been divided in two groups with respect to their BF. The cutoff frequency of 1.25 kHz was chosen on the basis of psychophysical results (Wiegrebe and Winter, 2001b). For IRN(−) the average response for units with BFs below 1.25 kHz showed a local minimum in the all-order ISIHs at d and the highest peak at $2d$. The chopper units with higher BFs show the highest peak at d. This data is consistent with the psychophysical results on pitch perception of IRN(−).

2. Methods

2.1. Physiology

Experiments were performed on pigmented guinea pigs (*Cavia porcellus*), weighing between 315 and 705 g. The animals were anaesthetized with urethane (1.5 g/kg, ip); Hypnorm was administered as supplementary analgesia (1 mg/kg, im). Anaesthesia and analgesia were maintained at a depth sufficient to abolish the pedal withdrawal reflex (front paw). Additional doses of Hypnorm (1 ml/kg) or urethane (1 ml) were administered on indication. Incisions were pre-infiltrated with the local anaesthetic Lignocaine