The responses of single units in the ventral cochlear nucleus of the guinea pig to damped and ramped sinusoids

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Abstract

Human listeners hear an asymmetry in the perception of damped and ramped sinusoids; the partial loudness of the envelope component is greater than the partial loudness of the carrier component for damped sinusoids. Here we show that an asymmetry also occurs in the physiological responses of most units in the ventral cochlear nucleus to these same sounds. The activity elicited by damped sinusoids is mainly restricted to the beginning of each envelope period, which is not the case for ramped sinusoids. This can be quantified by computing the ratio of the tallest bin of the modulation period histogram to the total number of spikes (the peak-to-total ratio, p/t). Damped sinusoids produce a higher p/t than ramped sinusoids, which demonstrates physiological temporal asymmetry. It is also the case that ramped sinusoids typically elicit more spikes than damped sinusoids. The physiological asymmetry occurs where the perceptual asymmetry is present. It is maximal at modulation half-lives of 4 and 16 ms, greatly reduced at 1 ms and absent at 64 ms. Different unit types exhibit differing degrees of temporal asymmetry. Onset units produce the greatest p/t asymmetry, primary-like units produce the least asymmetry and chopper units are in-between. With regard to total spike count, the maximal asymmetry occurs with chopper units. If primary-like units are assumed to reflect the activity in primary auditory nerve fibres, then there is enhancement of temporal asymmetry in the ventral cochlear nucleus by both onset and chopper units. © 2000 Elsevier Science B.V. All rights reserved.

Key words: Chopper unit; Onset unit; Primary-like unit; Brainstem; Temporal asymmetry; Amplitude modulation

1. Introduction

A sine wave that is asymmetrically amplitude-modulated by a periodic, decaying exponential (damped sinusoid) produces a two-component percept; a tonal component corresponding to the carrier and a drumming component corresponding to the envelope. When such a sound is reversed in time (ramped sinusoid), the relative strength of the two perceptual components changes dramatically. The tonal component increases whereas the drumming component decreases (Patterson, 1994a,b). Damped and ramped sinusoids pose an interesting problem for the understanding of temporal processing in the auditory system as their long-term spectra are identical and they contain two different periodicities (carrier and envelope) that are perceived simultaneously.

Patterson (1994a) first compared the perception of damped and ramped sinusoids by varying the half-life of the modulating exponential in order to determine the effect of the rate of rise/fall (see Fig. 1). He found that for half-lives from 1 to 32 ms, the damped and ramped sinusoids could be readily discriminated and that listeners consistently chose the ramped sinusoid as the one with the stronger tonal percept (percent correct > 90). For a 64 ms half-life, performance fell near to chance level. This result was obtained with carrier frequencies ranging from 400 to 4800 Hz. Patterson (1994b) then

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varied the modulation period along with the carrier period in order to keep a fixed number of carrier cycles per envelope period. It was concluded that psychophysical performance was better for low carrier frequencies than for high ones. Note, however, that for a constant modulation period the perceptual asymmetry increases with carrier frequency.

Irino and Patterson (1996) introduced another method to measure the perceptual asymmetry produced by damped and ramped sinusoids. They measured the half-life of a damped tone that would produce the same perceptual ratio of the drumming and tonal components as a given ramped tone. The study was done at a single carrier frequency of 800 Hz. Damped sinusoids always required a longer half-life to produce the same perceptual ratio, and with a ramped half-life of 4 ms the ratio was approximately 7 to 1. The results showed that the asymmetry was largest between 4 and 8 ms and decreased for very short (< 1 ms) or very long (> 16 ms) half-lives. Patterson and Irino (1998) compared the strength of the perceptual asymmetry with the physiological asymmetry that might be expected in the auditory periphery in a time–domain model of auditory processing (Patterson et al., 1995). They showed (a) that the asymmetry of the impulse response of the cochlear filter is small relative to the perceptual asymmetry, (b) that adaptation and suppression of the form observed in auditory nerve fibres enhance the temporal asymmetry between damped and ramped sounds, and (c) that the combined temporal asymmetry associated with filtering and adaptation was still not sufficient to explain the perceptual asymmetry. They then went on to argue that the asymmetry is enhanced further during the processes that convert the neural patterns of the auditory nerve into the representation that underlies the perceptions that we ultimately hear.

The temporal asymmetry of the impulse response of the cochlear filter is well documented (e.g. Carney and Yin, 1988). Similarly, post-stimulus–time histograms (PSTHs) of the responses of auditory nerve fibres and primary-like units of the ventral cochlear nucleus (VCN) to sinusoids show that the onset is enhanced before adaptation brings the response down to its asymptotic level. There are, however, very few studies comparing the responses to spectrally matched pairs of temporally asymmetric stimuli. The fact that the impulse response of the cochlear filter is temporally asymmetric means that most models predict that ramped sounds will produce more spikes than damped ones at the level of auditory nerve fibres. Similarly, inter-spike intervals corresponding to the carrier period are predicted to be more common in the ramped tone responses (Patterson, 1994b). In a behavioural study using the Goldfish (*Carassius auratus*), Fay et al. (1996) showed that ramped sinusoids were judged more similar to pure tones than their damped counterparts. In an accompanying physiological study, recordings were made from the saccular nerve and it was observed that damped sinusoids produced both fewer overall spikes and less synchronisation to the carrier frequency. Fay et al. (1996) attributed both of these changes to the depletion and replenishment of neurotransmitter at the hair cell/afferent fibre synapse. In preliminary studies we (Winter and Patterson, 1997; Winter et al., 1998) performed experiments in the ventral cochlear nucleus and inferior colliculus (IC) of the anaesthetised guinea pig using damped and ramped sinusoids, with a fixed carrier frequency of 800 Hz and half-lives of 1, 4, 16 or 64 ms. For half-lives of 4 and 16 ms, single units in the cochlear nucleus generally responded with more spikes to ramped sinusoids than their damped counterparts. While this was often the case in the responses of single units in the IC, some units in the IC responded to ramped sinusoids with 1 ms half-lives while not responding at all to their damped counterparts. A similar finding was observed in the auditory cortex of the marmoset (Lu et al., 1999).

In Patterson and Irino (1998) the limited enhancement provided by the peripheral auditory system provided the basis for their argument that there is another stage of enhancement located more centrally in the auditory pathway. Accordingly, we have chosen to measure the responses of units in the ventral cochlear nucleus to spectrally matched pairs of damped and ramped sinusoids with a range of half-lives to determine (a) whether they exhibit temporal asymmetry and (b) whether it is maximal in the range 4–16 ms as in the perceptual data. For simplicity, Patterson and Irino (1998) assumed that the enhancement was the same for all units, although the simulation was most appropriate for primary-like units. They also assumed that the temporal asymmetry would be uniform across best frequency. In this paper, we measure the asymmetry in the responses of three different types of units (onsets, choppers and primary-likes), and for a wide range of best frequencies, to assess the validity of their assumptions. We matched both the amplitude and carrier frequency of the stimuli to the unit's threshold and best frequency. This had the advantage of ensuring that we were measuring the asymmetry present at BF and at a constant level above the unit's threshold rather than at a constant output level. The results show that there is a clear hierarchy in the degree of asymmetry found in different unit types with increasing asymmetry from primary-like units to chopper units to onset units when looking at envelope statistics, and increasing asymmetry from onset to primary-like to chopper units when looking at the number of spikes. Moreover, consistent with the perceptual data, the asymmetry increased with best frequency.
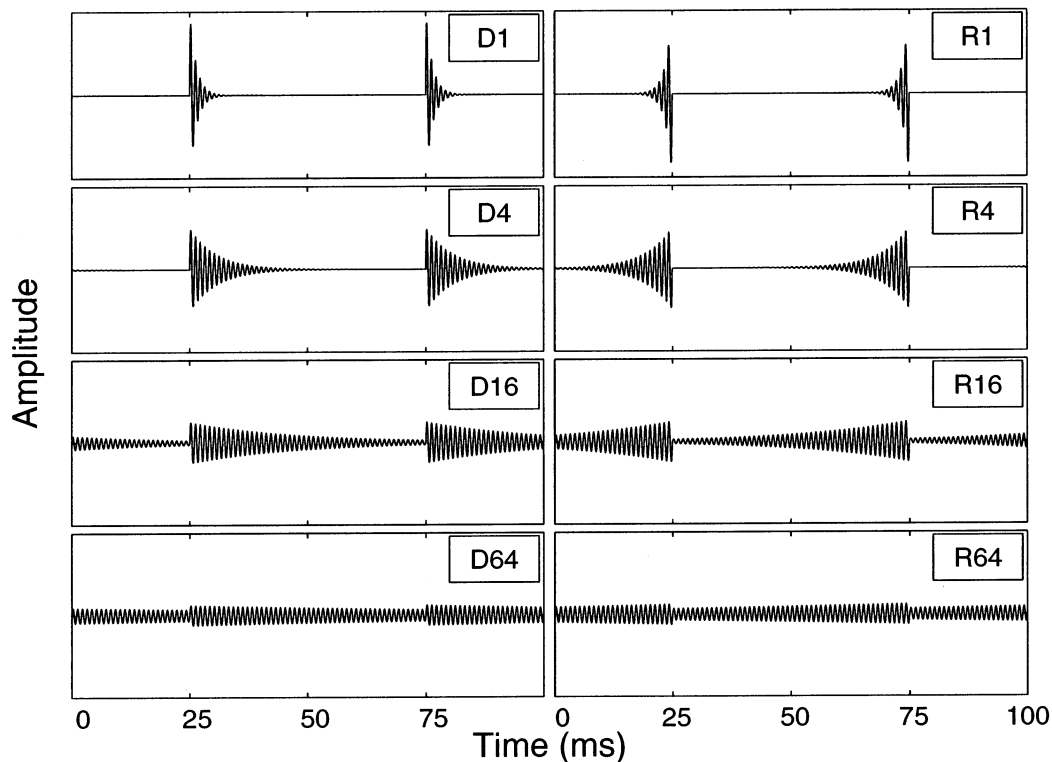
Fig. 1. Waveforms of damped and ramped tones. Damped sinusoids (D) are in the left column, ramped sinusoids (R) in the right column. The half-lives used in the experiments are displayed: 1, 4, 16 and 64 ms, as identified by the top-right insert on each panel. The carrier frequency in this example is 1 kHz. Carrier frequency was always adjusted to equal the unit best frequency. The modulation period was chosen to be the largest integer number of carrier periods less than or equal to 50 ms. Ten modulation periods were constructed, giving a duration of approximately 500 ms.

2. Materials and methods

2.1. Preparation

The data reported in this paper were recorded from 25, post-weaned (∼4–6 weeks of age), pigmented guinea pigs, weighing between 319 and 471 g. Animals were anaesthetised with urethane (1.5 g/kg i.p.) and supplementary analgesia provided by Hypnorm (1 mg/kg). All animals were given atropine sulphate (0.06 mg/kg, sc) as a premedication. Additional doses of urethane and analgesia were given when required.

The surgical preparation and stimulus presentation took place in a sound-attenuated chamber (IAC). All animals were tracheotomised and core temperature maintained at 38°C with a heating blanket. Following placement in the stereotaxic apparatus a midline incision of the scalp was made and the skin retracted laterally. The temporalis muscle on the left-hand side of the skull was removed and the bulla exposed. The method of stereotaxic positioning follows that previously reported (Winter and Palmer, 1990). No histological verification of recording position was undertaken but we are satisfied that all the units reported in this paper were recorded from the cochlear nucleus; the

stereotaxic coordinates were similar to those used in previous studies in the ventral and anteroventral cochlear nucleus (Winter and Palmer, 1990; Winter and Palmer, 1995; Palmer and Winter, 1992,1993) and electrode tracks sometimes coursed their way through the dorsal cochlear nucleus (DCN) before entering the ventral division. Although data were recorded from units in the DCN, as judged by their stereotaxic position and physiological response type (e.g. Stabler et al., 1996), we have excluded them from the present data sets. We acknowledge that it is possible we may have included chopper units located in the deep layers of the DCN, however, if this is the case they responded to both pure tones and ramped and damped sinusoids in an identical manner to their VCN counterparts.

The compound action potential (CAP) was monitored with the use of a silver coated wire placed on the round window of the cochlea. The signal was filtered and amplified ($\times 10\,000$). The CAP threshold was determined visually (10 ms tone pip, 1 ms rise/fall time, $10\ s^{-1}$) at selected frequencies at intervals during the experiment. If thresholds deteriorated by more than 10 dB and were not recoverable (for example, by removal of fluid from the bulla) the animal was killed by an anaesthetic overdose of sodium pentobarbital (i.p.).
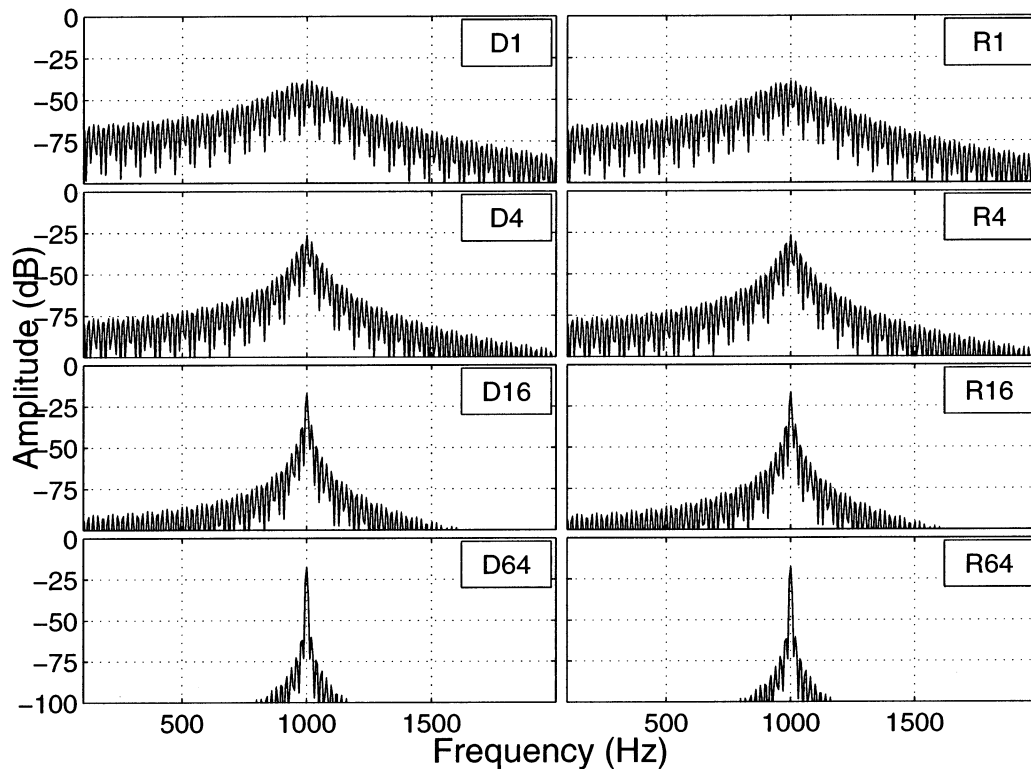
Fig. 2. Power spectra of damped and ramped sinusoids. The stimuli parameters are as in Fig. 1. To keep approximately constant energy between stimuli with different half-lives, the amplitude was normalised by a factor proportional to the square root of the half-life (see Eq. 1).

The experiments performed in this paper have been carried out under the terms and conditions of the personal and project licences issued by the United Kingdom Home Office to the second author.

2.2. Isolation of single units

Recordings were made using tungsten in glass microelectrodes (Merrill and Ainsworth, 1972). Electrodes were advanced by an electronic microdrive (Kopf 650 W) through the intact cerebellum in the sagittal plane at an angle of 45°. A wideband noise stimulus was used to locate the surface of the cochlear nucleus and to search for single units. Upon isolation of a single unit, estimates of best frequency (BF) and threshold were obtained using audio-visual criteria. The spontaneous discharge was measured over a 10 s period. Single units were classified by their peri-stimulus–time histogram shape in response to suprathreshold BF tone bursts, their inter-spike interval and discharge regularity (Young et al., 1988). To identify a unit as an onset unit we have used the classification scheme of Winter and Palmer (1995). PSTHs were generated in response to 250 short tone bursts (50 ms) at the unit's BF. Rise–fall time was 1 ms (cos^2 gate) and the repetition rate was 4 s^{-1}. The starting phase for each tone burst was randomly selected. Spikes were timed with 1 μs resolu-

tion (TDT ET1) and typically sound levels of 20 and 40 or 50 dB suprathreshold were used. All single tone PSTHs shown in this paper include a 20 ms delay before the onset of the stimulus.

2.3. Complex stimuli

The stimuli for the experiment were generated as follows. First, a pure tone of frequency, *fc*, was computed starting in sine phase. The frequency was the BF for each unit. Then, the amplitude envelope was constructed. The equation for one envelope cycle is given in Eq. 1.

$$E(t) = 1/\sqrt{(hl)}\cdot e^{-t\ln 2/hl} \tag{1}$$

with *t* the time within 0 and 1/*fm*, *hl* the half-life, and *fm* the modulation frequency. The modulation period 1/*fm* was chosen to be the largest integer number of carrier periods less than or equal to 50 ms. This ensured that the discontinuity in the envelope, that occurs at the end of each modulation cycle, occurs at an upward-going zero-crossing of the carrier. Ten modulation periods were constructed, giving a duration of approximately 500 ms. The amplitude was normalised by a factor proportional to the square root of the half-life. For human listeners this produces approximately con-
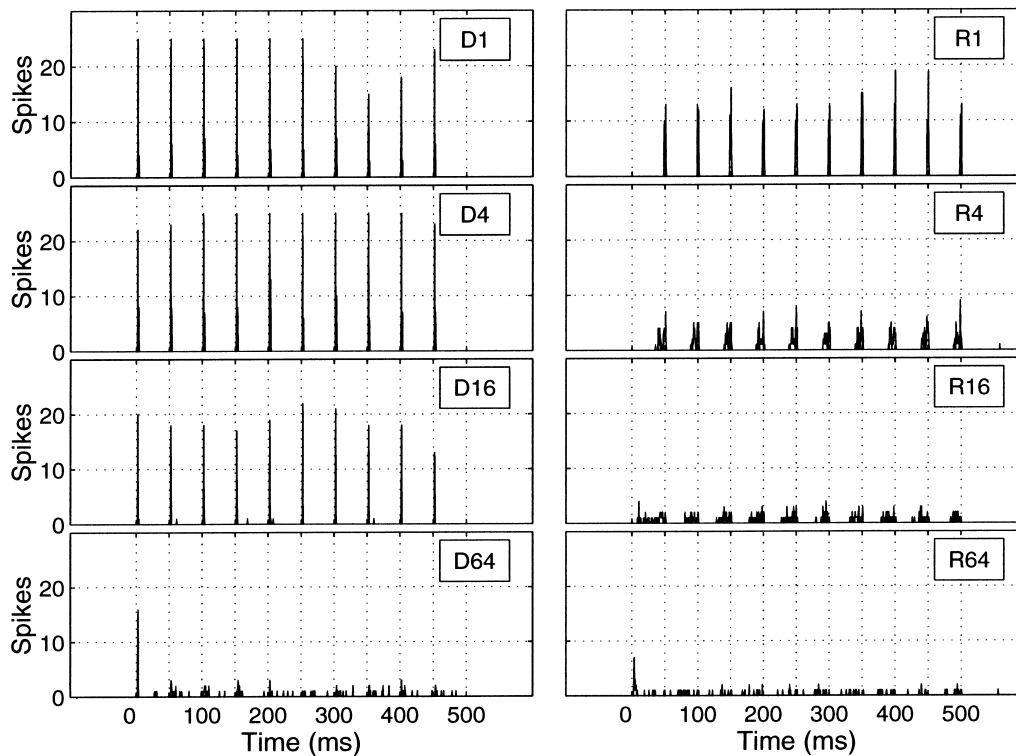
Fig. 3. Post-stimulus–time histograms in response to damped and ramped sinusoids. Unit 0255010010, BF = 3.12 kHz, pure-tone threshold = 45 dB SPL. Bin width is 500 μs, 25 repeats. Stimulus level was 15 dB above pure-tone threshold. This unit was classified as an onset chopper. Responses to damped sinusoids are limited to the beginning of each modulation cycle, whereas responses to ramped sinusoids are spread throughout the modulation cycle. Except for the first cycle, that may elicit an exaggerated onset (see D64), all modulation cycles display similar responses and may thus be collapsed into a modulation period histogram (see Fig. 4).

stant loudness across the stimulus set (Patterson, 1994a). Finally, the amplitude envelope and the sinusoid at *fc* were multiplied together to produce the given experimental stimulus. The half-lives were 1, 4, 16 and 64 ms. PSTHs were generated in response to 25 repetitions of the stimulus. This procedure ensured that 250 modulation periods were presented for each condition. The sampling rate was 50 kHz.

After digital-to-analog conversion, the stimuli were low-pass filtered at the Nyquist frequency (Stanford research systems dual-channel programmable filter, SR640). The stimuli were equalised (Phonics graphic equalizer EQ 3600) to compensate for the frequency response of the speaker and coupler before being fed into a Rotel RB871 power amplifier and a programmable final attenuator (0–75 dB in 5 dB steps). The signal was presented over a speaker (Radio Shack electrodynamic tweeter) mounted in a coupler designed for the ear of a guinea pig. The stimuli were acoustically monitored with a Bruel & Kjaer 4134 microphone attached to a calibrated 1 mm probe-tube. The sound level of the damped/ramped stimuli was chosen to be approximately 15 dB above each unit's threshold at BF. Waveforms and spectra of the stimuli for a 1 kHz carrier are shown in Figs. 1 and 2, respectively.

3. Results

The responses to damped and ramped sinusoids were recorded from 135 units. Single units were classified according to existing classification schemes (Young et al., 1988; Blackburn and Sachs, 1989; Winter and Palmer, 1995). Results will be presented for the three main classes of physiological response types, primary-like, chopper and onset. Eleven units did not fit easily into the above classification schemes and were labelled unusual; a further 12 units were classified as low BF as it was not possible to distinguish which category they belonged to because of phase-locking.

3.1. Responses of single units

3.1.1. Onset

There were 32 onset units including On (18), OI (1), OL (5) and OC (8) units (see Winter and Palmer, 1995, for details of the classification of the sub-types of the onset group).

Post-stimulus–time histograms of the responses of an OC unit to damped and ramped stimuli are presented in Fig. 3. They are clearly different. To quantify the difference, two statistics were derived from the PSTHs. The
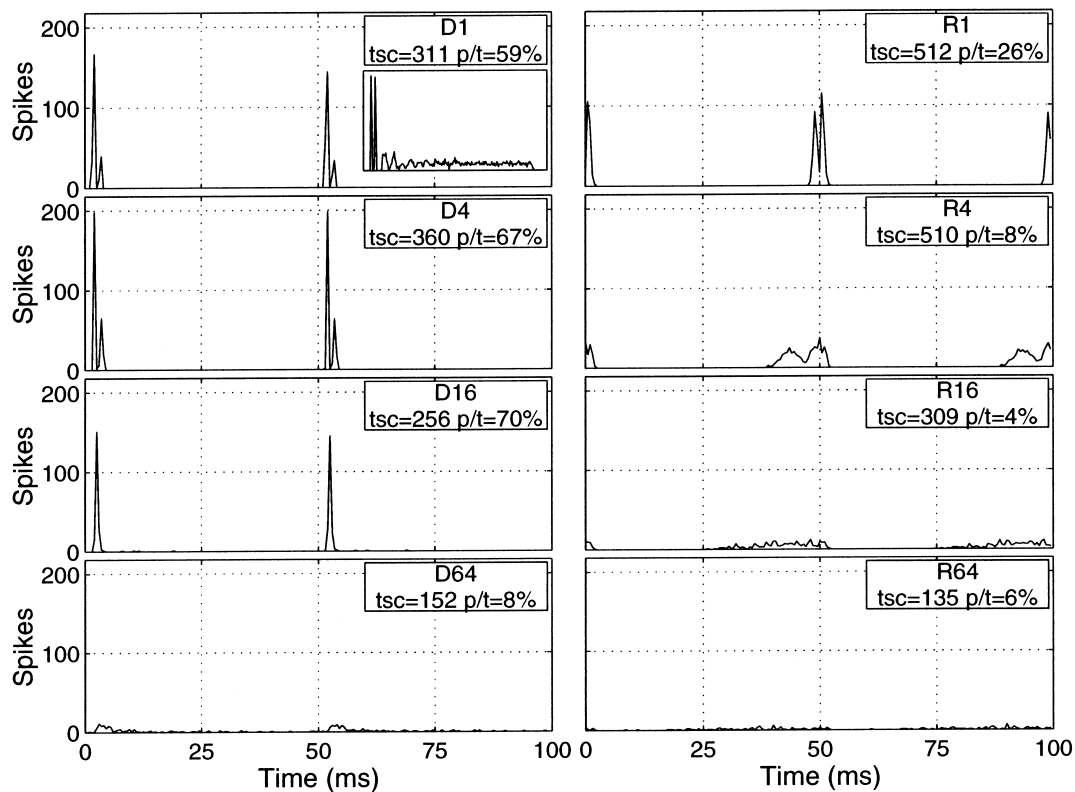
Fig. 4. Modulation period histogram for the onset chopper unit, shown in Fig. 3, in response to damped and ramped sinusoids. Two periods of the MPH are displayed for visual purposes (bin width is 500 μs). For each panel, the top-right insert identifies the stimulus condition (damped or ramped and half-life) and shows the corresponding MPH statistics (*tsc* and peak-to-total ratio). Compared to Fig. 3, this kind of display reveals the details of the response to one modulation cycle. In the panel labelled D1, an additional insert shows the PSTH of the unit in response to a 50 dB suprathreshold BF tone burst (bin width is 250 μs).

first statistic was simply the total number of spikes elicited in response to the 25 repeats of the ramped and damped stimuli and shall be referred to as total spike count or *tsc*. The second statistic is a measure of the 'peakiness' of the response to each modulation, calculated as follows. We transformed the PSTHs into modulation period histograms (MPHs), which are period histograms with a period equal to the modulation period, $1/fm$. Note that the first period of the PSTH response was left out of the MPH as its shape was often markedly different from the remainder and it might distort the measure of asymmetry (e.g. see Fig. 3, D64). We then calculated the peak activity divided by the total activity (*p/t*) for each damped/ramped pair. The peak was taken as the number of spikes in the highest MPH bin. If activity is restricted to a single bin, *p/t* is equal to 100%. If activity is evenly spread out throughout the modulation cycle, *p/t* is close to 0%. The bin width was 500 μs. Finally, for visual purposes, we display two-period MPHs obtained by computing period histograms synchronised to the modulation period, but with a two-period length. This sums up the response to the modulation by considering each

modulation cycle as a repetition (except for the first one, hence yielding a total of $25 \times 10 - 25 = 225$ modulation cycles) while ensuring that at least one uninterrupted cycle of modulation is visible in the figures.

The statistics and two-period MPHs thus obtained are presented in Fig. 4. The asymmetry in the responses to damped and ramped sinusoids for the same half-life is obvious in the MPHs and in the statistics. For instance at the 4 ms half-life (second row), the response to the damped tone had most spikes at the beginning of the modulation cycle, and the *p/t* is high, 67%. In strong contrast, the response to the ramped tone with the same half-life is relatively evenly distributed throughout the modulation cycle, and the *p/t* is low, 8%. The same pattern of response is observed for half-lives of 1 and 16 ms. It has largely disappeared for 64 ms. Another feature of the responses of this unit is that the *tsc* is larger for ramped than for damped stimuli for half-lives of 1, 4 and 16 ms. This unit was chosen as an example because it shows a particularly large asymmetry. The way the unit compares to other onsets as well as the variability of the *p/t* and *tsc* statistics is discussed in Section 3.2.
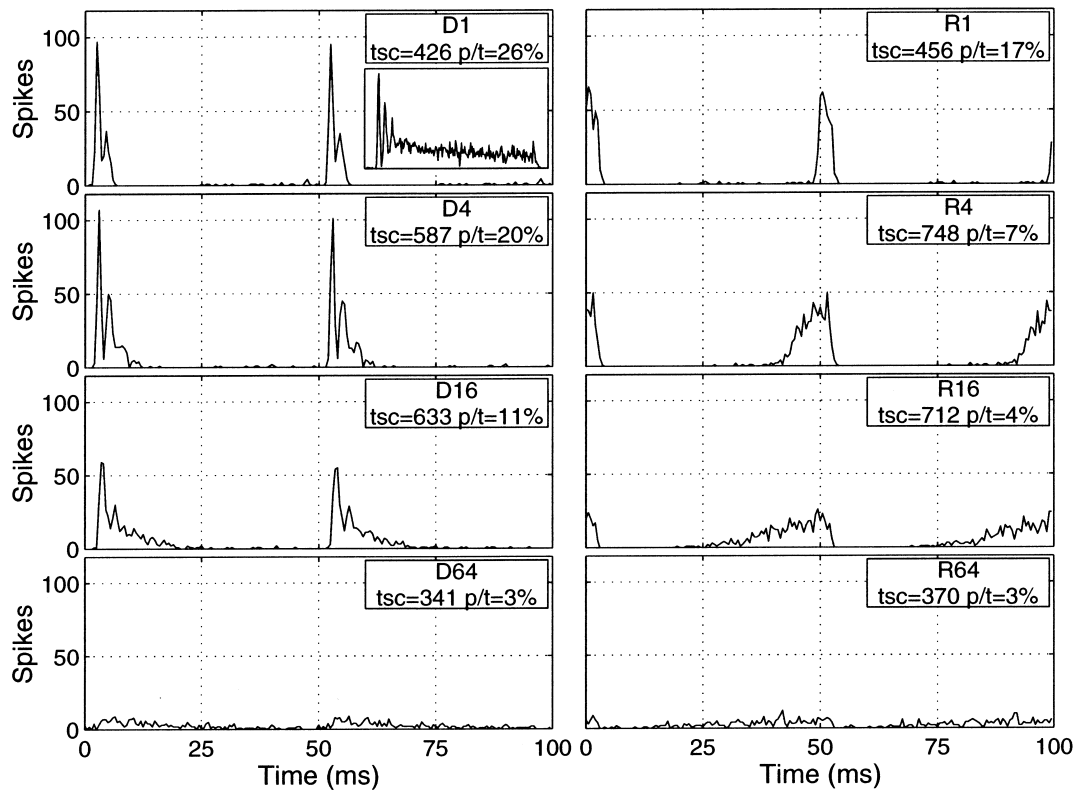
Fig. 5. Modulation period histogram for a transient chopper unit in response to damped and ramped sinusoids. Unit 0238013003, BF = 8.26 kHz, pure-tone threshold = 21 dB SPL. Format of figure is the same as Fig. 4, except that the pure-tone PSTH was obtained 20 dB above threshold.

3.1.2. Chopper

The chopper unit category has been divided into two. This was based on the discharge regularity in response to suprathreshold BF tone bursts. Units classified as sustained choppers (Chop-S) had a very regular discharge pattern and a coefficient of variation (CV) less than 0.35 whereas units classified as transient choppers (Chop-T) had a CV between 0.35 and 0.5 (see Young et al., 1988 for details). Chop-T and Chop-S units were first analysed separately. Although there was a trend on average for Chop-S units to produce more p/t asymmetry than Chop-T units, the distributions of the p/t and tsc asymmetry measures were not statistically different between the two unit types (Wilcoxon rank sum test, $P > 0.05$). All chopper units are thus considered together from now on, with respect to their responses to damped and ramped sinusoids. There were 38 chopper units including Chop-T (24) and Chop-S (14) units.

The results for a Chop-T unit are presented in Fig. 5. The pattern of responses again displays a clear asymmetry. The largest asymmetry appears for a 4 ms half-life. In response to damped sinusoids, the unit is chopping in response to each modulation cycle. For ramped sinusoids, the unit seems to be driven by the stimulus, thus obscuring the chopping response in the MPHs. The p/t asymmetry is less pronounced than in the case

of the onset units. The asymmetry in tsc is, on the other hand, larger than for onset units.

3.1.3. Primary-like

There were 32 primary-like units. The results for a typical unit are shown in Fig. 6. Compared to the chopper or onset responses, the asymmetry in the shape of the MPH is less pronounced. Apart from a difference at the onset of the modulation cycle, responses to damped and ramped sinusoids are almost time reversals of each other and the p/t is always low. There is also a small, but significant (see below) asymmetry in the tsc for most half-lives, however, it is less pronounced than for chopper units.

The primary-like unit type excludes primary-like with a notch, PN (8), as we found that their p/t asymmetry between damped and ramped responses was significantly greater at half-lives of 1, 4 and 16 ms than that observed with primary-like units ($P < 0.01$; Wilcoxon rank sum test). We have therefore excluded PN units from our population analyses. In support of this exclusion it is likely that PN and primary-like units form separate signal processing pathways; PN responses are recorded from globular bushy cells in the posterior anteroventral cochlear nucleus and project to the contralateral medial nucleus of the trapezoid body
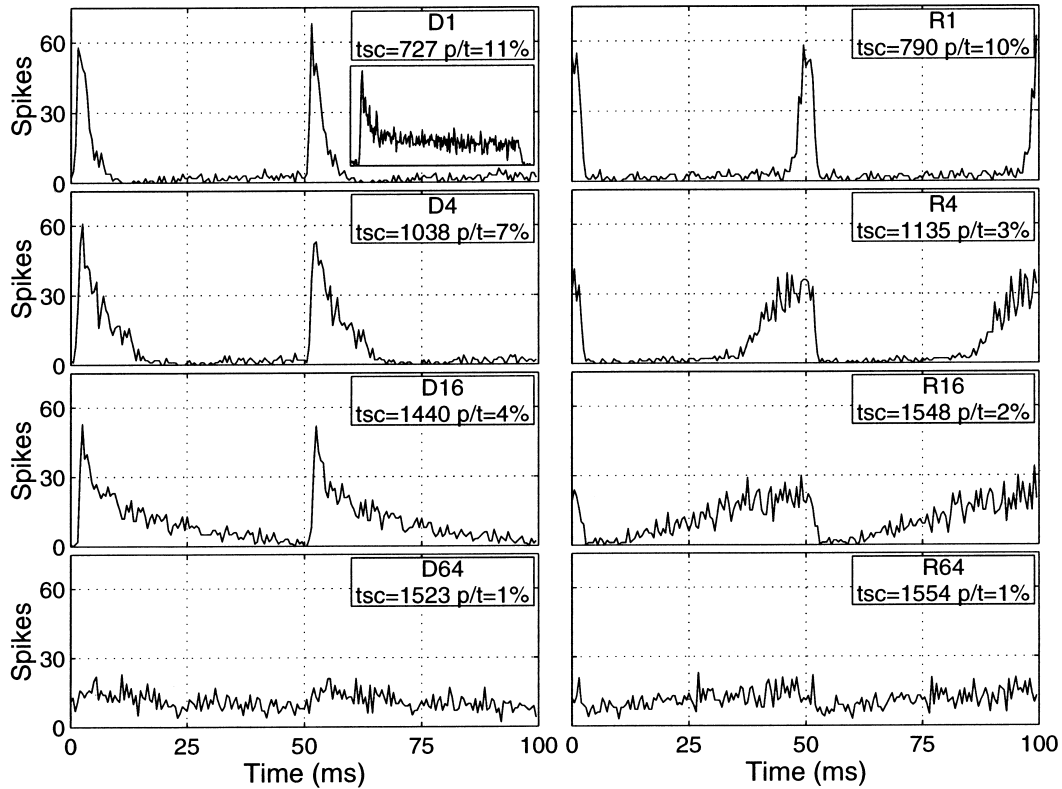
Fig. 6. Modulation period histogram for a primary-like unit in response to damped and ramped sinusoids. Unit 0250003002, best frequency 2.04 kHz, pure-tone threshold = 32 dB SPL. Format is the same as for Fig. 5.

(Smith et al., 1991; Spirou et al., 1990) whereas primary-like units are recorded from spherical bushy cells in the rostral pole of the anteroventral cochlear nucleus and project to areas predominantly outside the medial nucleus of the trapezoid body.

3.2. Population analyses

3.2.1. Asymmetry ratios

In order to quantify the temporal asymmetry across the population of neurones, ratios between response statistics to damped and ramped sinusoids were computed. As ratios were used, units that failed to produce a minimum number of spikes ($n = 10$) in every condition were omitted. The ratios were then computed for each unit and for each half-life. Population statistics were derived within each unit type (onset, chopper and primary-like).

The median p/t ratios for the three unit types are shown in Fig. 7 as a function of half-life. If there were no asymmetry, all of the data would fall on a horizontal line with a ratio of 1. The significance of the difference between a given asymmetry ratio and unity (no asymmetry) was estimated with a sign test of the median. There was a significant ($P < 0.01$) p/t asymmetry for all conditions except for onset and primary-like types at 64 ms, and the magnitude of the
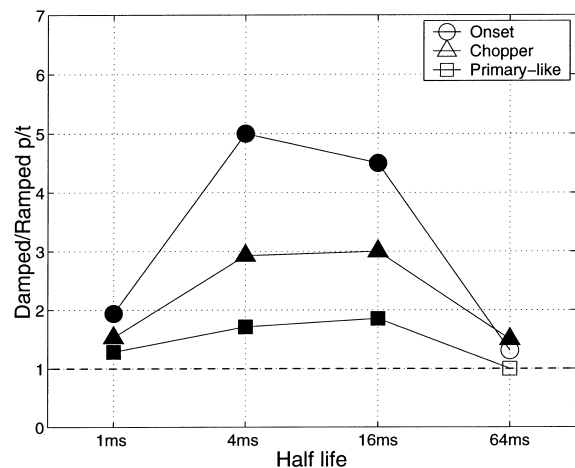

Fig. 7. Population analysis of the p/t asymmetry. For each half-life, the p/t obtained in response to the damped tone was divided by the p/t obtained in response to the ramped tone. Units that gave less than 10 spikes in any given condition were discarded. The analysis was done within each unit type: onset ($n = 26$), chopper ($n = 36$), primary-like ($n = 31$). Median results for each unit type and half-life are displayed. If no asymmetry was present in the p/t statistics, all points would fall on the horizontal line of unity. Filled symbols indicate a significant asymmetry ($P < 0.01$, sign test of median).
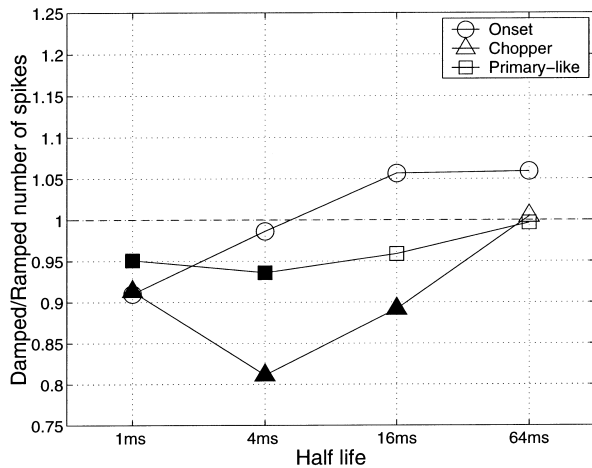
Fig. 8. Population analysis of the *tsc* asymmetry. For each half-life, the *tsc* obtained in response to the damped tone was divided by the *tsc* obtained in response to the ramped tone. Median results for each unit type and half-life are displayed. If no asymmetry was present in the *tsc* ratio statistic, all points would fall on the horizontal line of unity. Filled symbols indicate a significant asymmetry ($P < 0.01$, sign test of median).

asymmetry is strongly dependent on half-life. In all cases, a large asymmetry is observed at 4 and 16 ms, while little, or no, asymmetry is observed at 1 and 64 ms. The unit type also has an influence on the magnitude of the asymmetry. When the asymmetry is large, there is a clear hierarchy of unit types: onsets (∼ 5:1); choppers (∼ 3:1); and primary-like (∼ 2:1).

The median *tsc* ratios for the three unit types are shown in Fig. 8 as a function of half-life. Again, if there were no asymmetry, the data would fall on a horizontal line with a ratio of 1. In general, ramped sinusoids produce greater *tsc*'s than damped sinusoids and so the *tsc* ratio is typically less than unity. The significance of the asymmetry was estimated with the sign test of the median. There was a significant ($P < 0.01$) *tsc* asymmetry for chopper units at half-lives of 1, 4 and 16 ms, and for primary-like units at 4 and 16 ms. There is no significant asymmetry for onset units; the median ratio does sometimes show an asymmetry but the variability in *tsc* of these units is too large for the ratio to reach significance. The greatest asymmetry is observed for choppers at 4 ms (20% fewer spikes for the damped

Table 2
Difference in *tsc* asymmetry between unit types

Unit comparison	1 ms	4 ms	16 ms	64 ms
Onset/chopper	-	**	**	-
Onset/primary-like	–	–	*	**
Primary-like/chopper	–	**	**	–

Significance levels (Wilcoxon rank sum test) are indicated as follows: * = $P < 0.05$; ** = $P < 0.01$; – = $P > 0.05$.

responses). Choppers generally display the greatest asymmetry in *tsc*, followed by primary-likes.

3.2.2. Hierarchy of temporal asymmetry

Figs. 7 and 8 reveal an orderly hierarchy in the strength of the temporal asymmetry observed in the responses of the different unit types. To estimate whether the asymmetry differed significantly between unit types, pairwise Wilcoxon rank sum tests were performed between the distributions of ratios within each unit type, for each half-life separately. The results are shown in Tables 1 and 2. There are significant differences between the three unit types in their *p/t* ratios. Onsets exhibit the greatest asymmetry in *p/t* ratio, followed by choppers and primary-likes. In the case of the *tsc* ratio, there is a significant difference between choppers and primary-likes but in the opposite direction. Comparisons involving onsets often fail to reach significance because of the variability of the data.

3.2.3. Influence of unit best frequency

To determine whether there was an effect of carrier frequency in the physiological data, we computed correlations for the *p/t* ratio and the *tsc* ratio as a function of the logarithm of best frequency (BF). The results are presented in Table 3. There is a small but significant correlation between *p/t* ratio and log(BF) for 1, 4 and 16 ms; the higher the BF, the larger the asymmetry observed. The reason for this effect is probably the increase in auditory filter width with best frequency (Evans et al., 1989). Channels with wider filters preserve the modulation shape better and *p/t* is an envelope statistic. There is, however, only a weak correlation between the *tsc* ratio and BF.

Table 1
Difference in *p/t* asymmetry between unit types

Unit comparison	1 ms	4 ms	16 ms	64 ms
Onset/chopper	*	**	*	–
Onset/primary-like	**	**	**	*
Primary-like/chopper	*	**	**	**

Significance levels (Wilcoxon rank sum test) are indicated as follows: * = $P < 0.05$; ** = $P < 0.01$; – = $P > 0.05$.

Table 3
Correlation between asymmetry and the logarithm of unit best frequency

Asymmetry statistic	1 ms	4 ms	16 ms	64 ms
p/t	0.30**	0.31**	0.16**	0.08**
tsc	0.06*	0.06*	0.00–	0.00–

Significance levels (two-tailed Student's *t*-test) are indicated as follows: * = $P < 0.05$; ** = $P < 0.01$; – = $P > 0.05$.

4. Discussion

The results show that there is hierarchy of enhancement of temporal asymmetry in the responses of single units in the guinea pig's ventral cochlear nucleus. Onset units show the largest enhancement and primary-likes the smallest in terms of their p/t ratio. In terms of the tsc measure, units classified as choppers show the greatest temporal asymmetry with primary-like units again showing the smallest amount of asymmetry. The presence of temporal asymmetry in the cochlear nucleus is not in itself a surprise; most physical processes are temporally asymmetric. However, how the asymmetry develops through successive stages of the auditory pathway and how it relates to the observed perceptual asymmetry (Irino and Patterson, 1996) have important implications for neural models. In this section we briefly review physiological data from the literature on temporal asymmetry in the auditory pathway to compare it with the asymmetry observed in the three unit types encountered in the ventral cochlear nucleus. The data are then compared with the asymmetry measured at three stages of the auditory image model (AIM) by Patterson and Irino (1998). We show that there is already an enhancement of asymmetry in the VCN, a signal processing task which might previously have been associated with more central stages of auditory processing.

4.1. Temporal asymmetry in the peripheral auditory system

If a process converts a signal, A, such as a sound wave or a spike train, into a response, B, then that process is temporally *symmetric* if it also converts the time-reversed version of A into the time-reversed version of B. For example, a linear phase filter has a symmetrical impulse response and it does not introduce temporal asymmetry. All of the stages of peripheral auditory processing discussed in this paper produce at least some temporal asymmetry according to this definition. In this section, we review the stages and compare the degree of asymmetry at successive stages.

The first significant source of temporal asymmetry is the motion of the basilar membrane. At a given point on the membrane, the operation of the cochlea can be likened to that of a band-pass filter. de Boer and de Jongh (1978) and Carney and Yin (1988) recorded the responses of primary fibres to broadband noise and then using a reverse correlation (or 'revcor') technique they derived an estimate of the impulse response of the 'cochlear filter' at that point on the membrane. The envelope of the impulse response was found to be highly asymmetric, similar to a gamma function in which a rapidly rising power function is soon overpowered by a somewhat slower, decaying exponential. The temporal asymmetry inherent in this impulse response is quite typical of physical systems in general, and so temporal asymmetry was to be expected in cochlear filtering.

A second source of asymmetry is to be found at the level of the inner hair cell/afferent nerve fibre synapse. Adaptation is also inherently asymmetrical with rapid onset responses adapting eventually to an asymptotic level of response, so the transduction stage of auditory processing is another source of temporal asymmetry. We do not have any direct measurements of temporal asymmetry in auditory nerve fibres. We do, however, have responses from primary-like units in the cochlear nucleus which, as their name implies, typically produce similar responses to auditory nerve fibres. The p/t asymmetry in the population of primary-like units was 2 to 1 for damped over ramped sinusoids at the 4 ms and 16 ms half-lives.

The responses of the chopper and onset units reveal significantly greater p/t asymmetry than primary-likes. This enhancement fits with the basic properties of the unit response types. Onsets enhance the representation of the beginning of a sound, as a consequence, they will elicit a small number of spikes almost every time at the beginning of a damped modulation cycle but remain quiet for the rest of the modulation. For ramped sinusoids, the onset of the modulation is much less clear and activity will be distributed throughout the cycle. Chopper units respond to a damped modulation cycle with a response similar to that produced by an unmodulated sinusoid, that is, a spike train with ISIs around the chopping rate. For ramped sinusoids, the chopping response is less salient and the general spike responsiveness seems to be driven by the increasing amplitude of the stimulus. The physiological basis of the asymmetry enhancement (onset and chopper) is still unclear. It may derive from intrinsic membrane properties or it may involve inhibition from other units.

The asymmetry measured for most units at the level of the VCN is comparable to that observed perceptually in that it has the correct form as a function of half-life and carrier frequency. With both the p/t and the tsc statistics, for both unit types, the largest asymmetry was always associated with half-lives of 4 and 16 ms; a small asymmetry was observed at 1 ms, and no asymmetry remained at 64 ms (Figs. 7 and 8). The asymmetry also increased with carrier frequency (Table 3). All of this is qualitatively consistent with the psychophysical data (Patterson, 1994a,b; Irino and Patterson, 1996). Thus, it appears that the greatest asymmetry observed physiologically in the VCN of the guinea pig occurs when the largest asymmetry is reported by human listeners.

4.2. Computational models of temporal asymmetry

Time–domain computational models of auditory processing which begin with some form of auditory filter-bank have inherent temporal asymmetry. Patterson and Irino (1998) compared the asymmetry produced by a number of these models at the output of the cochlear filtering simulation, the neural transduction simulation, and a third, more central, stage developed to simulate the auditory image that we perceive in response to a sound. The models involved two alternative forms of cochlear simulation – either a gammatone auditory filterbank or an active transmission-line filterbank; two forms of neural transduction – the Meddis (1986) hair cell or 'two-dimensional adaptive thresholding'; and two forms of auditory image stabilisation – autocorrelation or 'strobed temporal integration'. All of the modules are described in Patterson et al. (1995) along with their computational implementations and applications. Patterson and Irino (1998) found that neither of the cochlear filterbanks on its own, or in combination with either of the transduction modules, produced sufficient temporal asymmetry to account for the perceptual asymmetry reported by Irino and Patterson (1996). They argued that a more central process must enhance temporal asymmetry further to account for the perceptual asymmetry. They do not, however, specify the location of the more central process; it was simply beyond the neural transduction stage.

The main aspect of the current physiological data is that there is prominent temporal asymmetry at the level of the CN, and even at this early stage in the auditory pathway there are many units with a degree of temporal asymmetry that is qualitatively consistent with that observed perceptually. It is not possible to decide which unit type best fits the perceptual asymmetry, as this would depend on the physiological response statistic chosen as the correlate for the perceptual data. Also, it is likely that the asymmetry is further processed through the higher stages of the auditory pathway. Preliminary single-unit recordings indicate that asymmetry to damped and ramped sinusoids persists at the level of the IC in guinea pigs (Winter et al., 1998) and in the primary auditory cortex of the marmoset (Lu et al., 1999). Whether significant differences exist in the responses to temporally asymmetric sounds between the CN, IC and auditory cortex remains to be determined.

4.3. Amplitude modulation encoding

Amplitude modulation is a common feature of natural sounds. For humans, modulation of a spectrally flat band of noise with the envelope of a speech signal can support recognition performance at above-chance levels in a limited context (Shannon et al., 1995). For animal calls, it may make communication in a noisy environments more robust (Nelken et al., 1999). The physiological encoding of amplitude modulation has been widely studied at the level of the CN (e.g. Møller, 1972). Frisina et al. (1985, 1990a,b) and Kim et al. (1990) showed that the temporal modulation transfer functions (tMTFs) of chopper units in the PVCN display an enhancement of AM compared to the auditory nerve and have a band-pass characteristic with respect to modulation frequency. Onset units display an even larger enhancement of AM, although their tMTF is broader than for chopper units (Frisina et al., 1985) or even low-pass (Rhode and Greenberg, 1994). These results led to the proposition that amplitude modulation might be encoded in the auditory system by means of a set of neurones tuned to a range of modulation frequencies, the temporal tuning possibly being transformed into a rate-place code after the CN (Langner and Schreiner, 1988; Langner, 1992).

Our results suggest that onset and chopper units are sensitive to another aspect of amplitude modulation and that is temporal asymmetry. A set of neurones rate-tuned to modulation frequencies would provide a representation of the power spectrum of the modulation. The sensitivity to temporal asymmetry indicates that the auditory system is also sensitive to the *phase* of the modulation spectrum (Pressnitzer and McAdams, 1999). Phase sensitivity cannot be observed in the responses to sinusoidally amplitude-modulated tones, so previous work is limited in this respect. Temporal asymmetry as observed in the present data would enhance onsets at the expense of offsets, which are ecologically less informative about the nature of the sound source (Saldanha and Corso, 1964), so this aspect of modulation sensitivity should probably be pursued.

4.4. Conclusion

Temporal asymmetry is a ubiquitous property of auditory processing. It can be observed in the motion of the basilar membrane, the adaptation of primary auditory fibres, primary-like, onset and chopper units of the CN, units of the central nucleus of the IC, and single units of auditory cortex. Moreover, temporal asymmetry is ubiquitous in the communication sounds of animals. Enhanced responses are observed in single units at the beginning of a sound event. They are also observed at the beginning of syllables in speech or animal communication sounds (Wang et al., 1995) and at the beginning of each glottal pulse in a vowel sound (e.g. Kim et al., 1986). Wang et al. (1995) have shown that single units in the primary auditory cortex of marmosets respond strongly to natural communication calls, but only weakly to the same call time-reversed. Our results suggest that processing at the level of the

CN may also be important in the encoding of asymmetry in complex sounds.

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