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Auditory processing of complex sounds: an overview

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SUMMARY

The past 30 years has seen a remarkable development in our understanding of how the auditory system – particularly the peripheral system – processes complex sounds.

Perhaps the most significant has been our understanding of the mechanisms underlying auditory frequency selectivity and their importance for normal and impaired auditory processing. Physiologically vulnerable cochlear filtering can account for many aspects of our normal and impaired psychophysical frequency selectivity with important consequences for the perception of complex sounds.

For normal hearing, remarkable mechanisms in the organ of Corti, involving enhancement of mechanical tuning (in mammals probably by feedback of electro-mechanically generated energy from the hair cells), produce exquisite tuning, reflected in the tuning properties of cochlear nerve fibres.

Recent comparisons of physiological (cochlear nerve) and psychophysical frequency selectivity in the same species indicate that the ear's overall frequency selectivity can be accounted for by this cochlear filtering, at least in bandwidth terms.

Because this cochlear filtering is physiologically vulnerable, it deteriorates in deleterious conditions of the cochlea – hypoxia, disease, drugs, noise overexposure, mechanical disturbance – and is reflected in impaired psychophysical frequency selectivity. This is a fundamental feature of sensorineural hearing loss of cochlear origin, and is of diagnostic value.

This cochlear filtering, particularly as reflected in the temporal patterns of cochlear fibres to complex sounds, is remarkably robust over a wide range of stimulus levels. Furthermore, cochlear filtering properties are a prime determinant of the 'place' and 'time' coding of frequency at the cochlear nerve level, both of which appear to be involved in pitch perception.

The problem of how the place and time coding of complex sounds is effected over the ear's remarkably wide dynamic range is briefly addressed.

In the auditory brainstem, particularly the dorsal cochlear nucleus, are inhibitory mechanisms responsible for enhancing the spectral and temporal contrasts in complex sounds. These mechanisms are now being dissected neuropharmacologically.

At the cortical level, mechanisms are evident that are capable of abstracting biologically relevant features of complex sounds.

Fundamental studies of how the auditory system encodes and processes complex sounds are vital to promising recent applications in the diagnosis and rehabilitation of the hearing impaired.

1. INTRODUCTION

In the Prado Museum in Madrid are five paintings by Brueghel de Velours, each illustrating one of the senses. The painting on hearing (*El oido*) depicts the problems this volume is concerned with. It shows our ears assailed by competing, complex sounds arising from many different sources: environmental, musical, speech and so on. Our ears have the task of separating the sources and analysing the individual sounds. Both binaural and monaural cues are involved; this conference and hence this overview concentrates on monaural processing.

If we take speech (figure 1) as a paradigm of a complex sound, it is characterized by bands of energy spanning multiple frequencies (e.g. the consonants and vowel of figure 1) and changing in frequency and amplitude with time (particularly the component frequencies – formants – of the vowel). The ear has at least three tasks to perform on a complex sound. First, to separate out the individual frequency components from several, simultaneously present (for example the vowel formants). This is termed frequency selectivity (or frequency analysis or resolution): the ability of the ear to resolve (breakdown) a complex sound into its individual, component frequencies. The spectral complexity of the stimulus, thus analysed, is the main determinant of its perceived timbre. It is also important, together with temporal cues, for determining the pitch of a complex sound (for speech, the perceived laryngeal frequency) and this information is essential in enabling the auditory system to differentiate between speakers. The second task for the ear is to enhance the spectral and temporal contrasts of the resolved frequency components in order to compensate for poor signal-to-noise-ratios in naturally occur-

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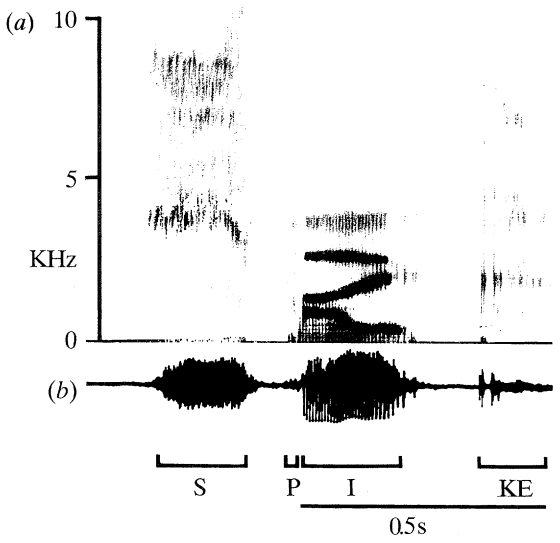

Figure 1. Frequency and time representation of the word 'spike'. (*a*) Spectrogram; (*b*) waveform. (From Evans 1974*a*.)

ring sounds, and to aid the third taks: namely to extract and abstract the behaviourally meaningful cues from the results of the peripheral spectral analysis. As far as behaviourally meaningful complex sounds like speech are concerned, this includes determining the spacing of the frequency components and their changes in time.

Where is all this carried out? Figure 2 shows a highly schematic summary diagram of the major components of the monaural auditory system.

1. The outer ear and middle ear act as signal 'conditioners', i.e. they emphasize those frequencies that are of most relevance for the particular species: for example, for humans about 1–3 kHz, for cats and guinea-pigs, about 5–15 kHz.
2. The cochlear partition in the inner ear or cochlea. This is the frequency analyser of the auditory system. The basilar membrane and the organ of Corti together perform the function of a distributed filter bank from which tuned channels emerge in the form of the responses of the cochlear nerve fibres.
3. The cochlear nerve fibres encode the filtered responses in terms of their spatio-temporal patterns of discharges in a cochleotopic ('tonotopic') map of activity across the array of tuned fibres emanating from the apical (low-frequency) to basal (high-frequency) end of the cochlea.
4. These filtered responses are passed on, in parallel, to a number of subsystems within the brainstem nuclei: starting with the cochlear nucleus (CN) where between two (shown here) or more likely three or more independent processing pathways diverge.
5. How far the subsystems are kept separate as we ascend the auditory midbrain is not clear. Nor do we have as clear a picture of the segregation function in the auditory cortex as in the visual system (except perhaps in the bat, thanks to Suga (this symposium)).

Unlike Brueghel, I have time only to paint a picture of the auditory system using rather broad brush

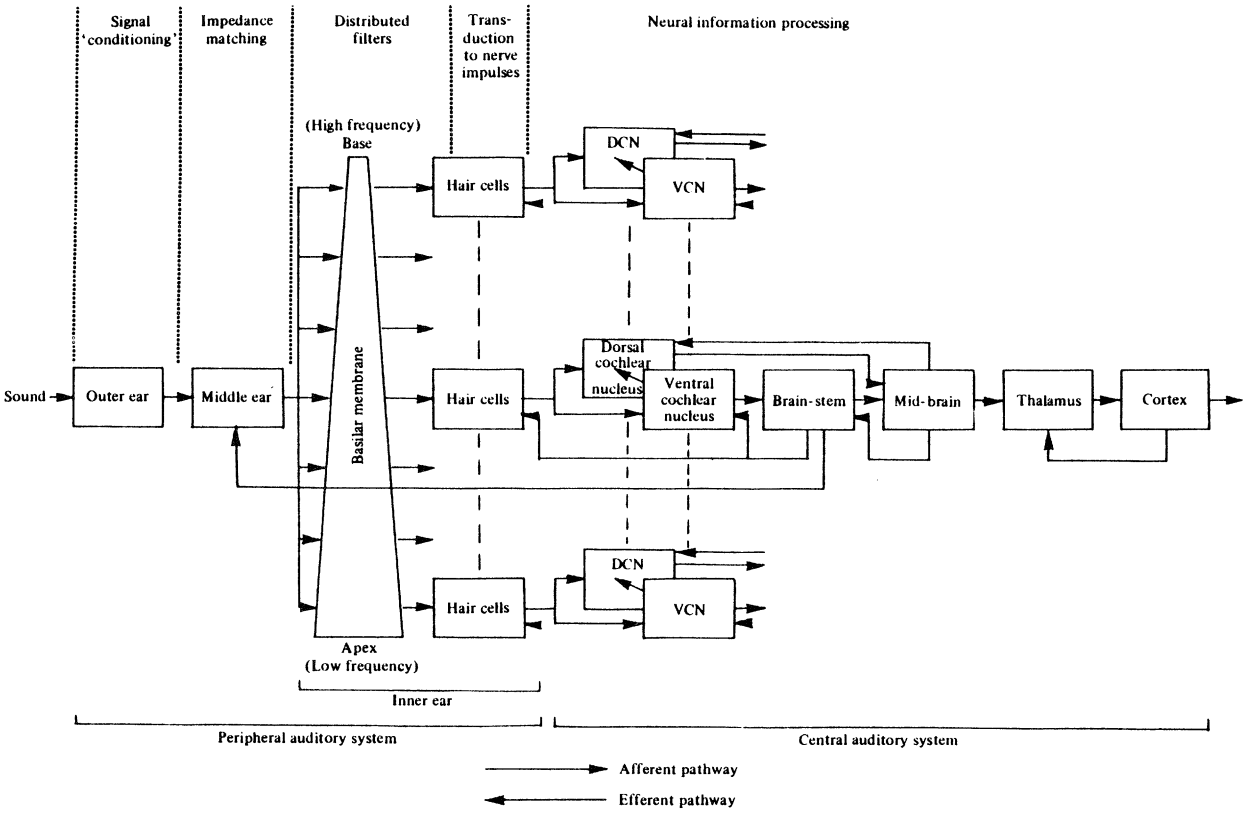

Figure 2. Schematic anatomical and functional map of the auditory sytem. (From Evans 1982.)

strokes. I will restrict my painting to a rather personal caricature of the three most clearly identified functions of the monaural auditory system at the three sites that have interested me over the last 30 years: the cochlear nerve, cochlear nucleus and auditory cortex. In so doing, I hope to emphasize a striking contrast in response properties that exists between cochlear nerve and cortical levels. To use a musical analogy, the response characteristics of the auditory periphery resemble those of a piano; of the cortex, those of a symphony orchestra!

2. PERIPHERAL FREQUENCY ANALYSIS SEEN AT THE LEVEL OF THE COCHLEAR NERVE

Central to our understanding of how the ear analyses complex sounds at this level into their component frequencies (frequency selectivity), is the physiological tuning curve of an individual fibre in the cochlear nerve (continuous curve in figure 3). The frequency threshold (or tuning) curve (FTC) describes the threshold sound intensity required to elicite a minimal response from the cochlear nerve fibre (an increase in the spike discharge rate) as a function of frequency. Under normal conditions (curve A in figure 3), the response of cochlear nerve fibres is very sharply tuned: they represent exquisitely tuned filters with bandwidths of the order of one sixth of an octave and cut-off slopes of several hundred dB per octave (see Evans (1975a) for review).

In the early 1970s I showed that this tuning was physiologically vulnerable. For example, a reduction in the oxygen supply to the cochlea could change the tuning from sharp and low threshold (curve A in figure 3), progressively (curves B–D) to blunt and high threshold (curve E). This was one of the lines of evidence that led to the proposal (Evans 1972) of the existence of an additional, biologically active (i.e. physiologically vulnerable) process sharpening up the relatively poorly tuned (passive) mechanics of the basilar membrane. We called it the cochlear 'second filter' as an expression of ignorance of the underlying mechanisms, but favoured (Evans 1972) a positive feedback process first proposed by Gold (1948; admittedly on spurious psychophysical evidence: see Evans (1975*a*)). At the time, all the evidence (poor basilar membrane tuning) pointed against a 'parallel' filtering enhancement process but supported a 'serial' process (see Evans & Wilson, 1973, 1975). The nature of the 'second filter' hypothesis has been much misunderstood and it perhaps needs to be emphasised that in its original framing it was sufficiently wide to embrace both 'parallel' and 'serial' filtering processes. Indeed, the validity of the extant mechanical data was specifically questioned (Evans 1972, 1975*a*). Furthermore, our studies of the influence of kanamycin poisoning of the cochlea (Evans & Harrison 1976; Harrison & Evans 1977) provided clear evidence that the integrity of the outer hair cells was crucial to sharp tuning of the cochlear nerve fibres emanating from the inner hair cells. For the mammalian cochlea, it now looks as though a parallel, physiologically active, enhancement process is required, involving the outer hair cells as the producers of motile energy coupling back to the inner hair cells (and to the basilar membrane, thus imparting sharp tuning to its mechanics: Sellick *et al.* (1982) in the guinea pig; Khanna & Leonard (1982) in the cat). On the other hand, for reptilian inner ears (where basilar membrane tuning is poor or negligible), a serial process appears to be involved, with electromechanical tuning of the hair cells themselves: see, for example, Crawford & Fettiplace (1981).

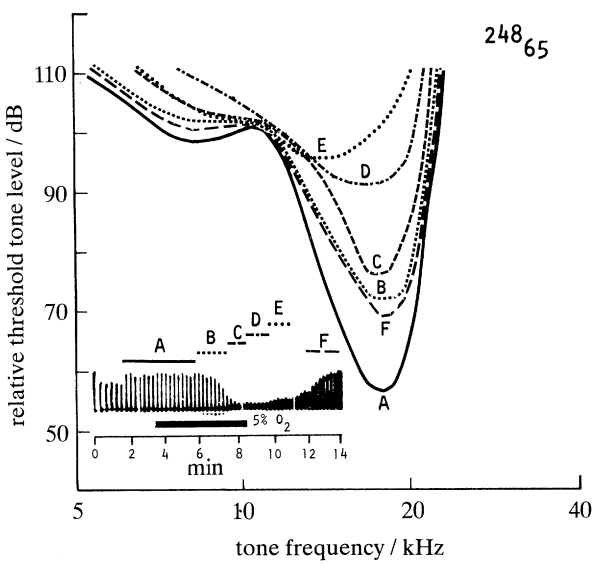

Figure 3. The effect of hypoxia on the tuning of a single cochlear nerve fibre. Curve A: frequency threshold curve (FTC) of cat cochlear nerve fibre. Curves B, C, D, E and F: FTCs obtained during and following 4 min hypoxia produced by reducing the expired air oxygen concentration to 5%. Inset shows timing of collection of FTC data in relation to the period of hypoxia and the brief reversible reduction in amplitude of the gross cochlear action potential in response to a fixed amplitude click. (From Evans 1974*b*.)

These frequency threshold curves can be considered to represent filters passing most energy at the characteristic frequency (CF): the most sensitive frequency, and least energy at frequencies further away. One of the remarkable things about these filters is that in spite of their resulting from nonlinear processes in the cochlea, they act surprisingly linearly in response to complex, i.e. multicomponent stimuli. In other words, their responses to these stimuli can be predicted to a first approximation over a surprisingly large dynamic range, by models containing linear band-pass filters having the same amplitude characteristics as the FTC (see Evans (1975*a*, 1989*a*) for reviews; see also Evans (1977, 1981, 1985*a*)).

Wilson and I first showed 20 years ago (Wilson & Evans 1971; Evans & Wilson 1973) that the characteristics of these physiological filters in the cat accounted approximately, but not exactly, for several aspects of psychophysical human frequency selectivity. Since then, Pickles (e.g. 1975) has questioned this conclusion, based on comparisons between his behavioural critical band data and our cochlear fibre data, both in the cat. Recently, I have had the opportunity

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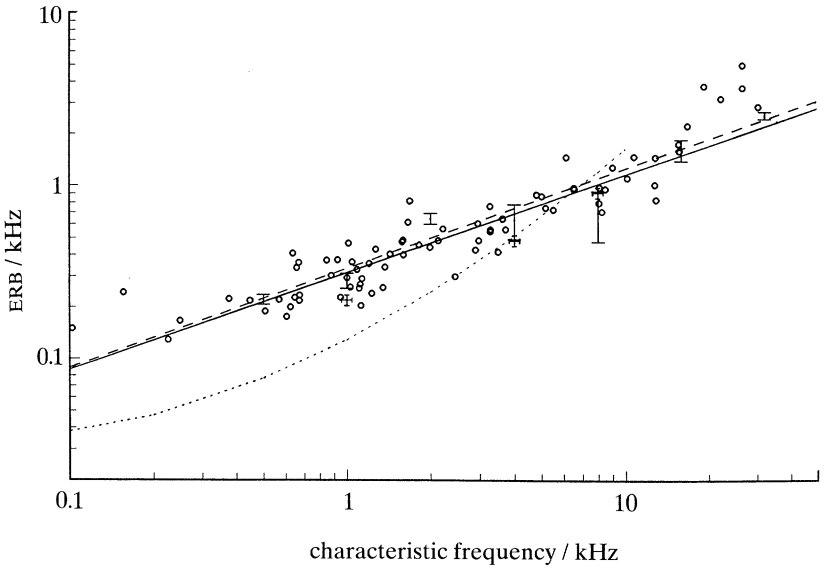

Figure 4. Comparison of behavioural and physiological frequency selectivity in the guinea-pig. Open circles: equivalent rectangular bandwidths (ERBs) of guinea-pig cochlear nerve fibres recorded under optimal conditions, i.e. with systemic arterial blood pressure 60 mm hg and gross cochlear action potential threshold 35 dB p.e. SPL. Bracket symbols: behavioural equivalent rectangular bandwidths derived from comb-filtered noise masking ±1 s.e. Star points: behavioural equivalent rectangular bandwidths derived from brandstop noise masking. The continuous line is the regression line through the mean equivalent rectangular bandwidths determined by comb-filtered noise masking. The dashed line is the regression line through the physiological data points. The dotted line represents human equivalent rectangular bandwidths from a variety of sources summarised in Moore *et al.* (1983). (From Evans *et al.* 1989, 1992.)

to make more appropriate comparisons between physiological and psychophysical selectivity in the guinea-pig (Evans et al. 1989, 1992). To make these comparisons, we make the assumption (mentioned above) that the physiological FTCs represent linear filters, and express the bandwidth of these filters as the width of a rectangular filter having the same area when the FTCs are plotted on linear power, linear frequency coordinates: the equivalent rectangular bandwith (ERB). Figure 4 shows the excellent agreement obtained between the ERBs of 80 single fibres in the guinea-pig cochlear nerve (open circles) compared with behavioural measurements of frequency selectivity in the same species, using comb-filtered noise masking and band-stop (notch) noise masking (bracket and cross symbols respectively). The good correspondence between the physiological and psychophysical data led us to hypothesize that the ear's overall frequency selectivity was already largely determined by peripheral mechanisms: by the exquisite tuning of the cochlea. An important consequence of this, and of the physiological vulnerability of cochlear tuning, is that when the function of the cochlea is impaired, through disease, drugs, mechanical or surgical damage, the ear's overall (psychophysical) frequency selectivity is likewise impaired (see Evans (1975*b*, 1978*b*) for review), and tests of frequency selectivity may, under certain conditions, be more sensitive tests of damage to the inner ear than conventional tests (e.g. West & Evans 1990).

Thus, in principle at least, the distributed filter bank of cochlear nerve fibres maps peaks of energy in the spectrum of the incoming sound into peaks of activity in the array of cochlear nerve fibres emanating from the cochlea. This is the place representation of a complex sound. However, as has been indicated, in impairment of cochlear function, deterioration in cochlear tuning will produce a blurred place representation of the spectrum of the incoming sound. This is why linear amplification, as in conventional hearing aids, though making the speech audible, will not make it any clearer (Evans 1978*b*; Pick & Evans 1982).

Similar blurring of the place representation occurs as a result of a severe nonlinearity in normal cochlear nerve fibre responses, namely the restricted dynamic range of most fibres. The range of sound intensities capable of eliciting changes in discharge rate with change in sound level is limited to about 40 dB in most cochlear fibres (Sachs & Abbas 1974; quantified as to proportions in Evans & Palmer (1980)). Because of this restriction, the mapping of activity in terms of discharge rate across place in the responses of the majority of cochlear nerve fibres is blurred out completely at moderate to high sound pressure levels (see Evans (1981) for review). However, Sachs & Young (1979), and Palmer & Evans (1979) have shown, in the cat, and Winter *et al.* (1990) in the guinea-pig, that this is not true of all cochlear nerve fibres: a small minority have (somewhat) higher thresholds than average and much wider dynamic ranges (not less than 70 dB), so that they are in principle capable of representing the spectra of complex stimuli on a rate place basis. This subset of cochlear nerve fibres account for some 5% of the total population: they are a sub-population of fibres having the lowest or no spontaneous discharge rates (Evans &

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Palmer 1980; Schalk & Sachs 1980). Liberman (1978) was the first to show that the cochlear nerve is not a homogeneus population of fibres: at least two (or three) sub-populations exist: a small low spontaneous rate population having higher thresholds and wider dynamic ranges; the remainder having the higher spontaneous rates, lower thresholds and dynamic ranges restricted to 40 dB on average (Liberman 1978; Evans & Palmer 1980; Schalk & Sachs 1980).

This minority population is capable of acting as rate place encoders of absolute spectral level at moderate to high stimulus levels. Although this situation can be adequate for models of intensity coding (Viemeister 1988), it does not seem very parsimonious for the great majority of cochlear nerve fibres not to be involved in coding the spectra of complex sounds at moderate to high levels. On the other hand, the presence of background noise can shift the dynamic ranges of cochlear nerve fibres (Evans 1974*b*; Costalupes *et al.* 1984), particularly when the effects of the descending, efferent projections to the cochlea are taken into account in the unanaesthetized preparation (May & Sachs 1992).

Looking for alternatives to rate processing, the potential for encoding complex sounds over a wide dynamic range has been explored in terms of the temporal discharge patterns of cochlear fibres. The important point here is that the timing of cochlear nerve fibre discharges to frequencies up to about 5 kHz or so is related to the period or multiples of the period of the stimulus. This is termed the 'phase locking' of the discharges to the stimulus waveform, and represents the basis of time representation theories of encoding frequency.

By using measures of the degree of phase locking as a function of the frequencies corresponding to the place of activity, Young & Sachs (1979) showed very beautifully that it was possible to extract the spectrum of speech vowels from the temporal discharge patterns of cochlear nerve fibres over a very wide dynamic range, including sound pressure levels well above those at which the discharge rate profiles of most were saturated and blurred out. Whether or not the higher levels of the auditory system can extract this representation, however, is still not clear.

What is clear however, is that the tuning of cochlear nerve fibres is surprisingly well represented in the temporal discharge patterns of cochlear nerve fibres over a very wide dynamic range (figure 5). These are the plots of the tuning of three cochlear nerve fibres (having relatively low, medium and high CFs) at low (lower half of figure 5) and high (upper half) intensities, obtained with a variety of complex stimuli. The measures of tuning have been extracted from the weighting or degree of phase-locking of the cochlear nerve fibre to individual component frequencies of a complex stimulus generated either by click trains (plus symbols), tone complexes (open circles) or broadband

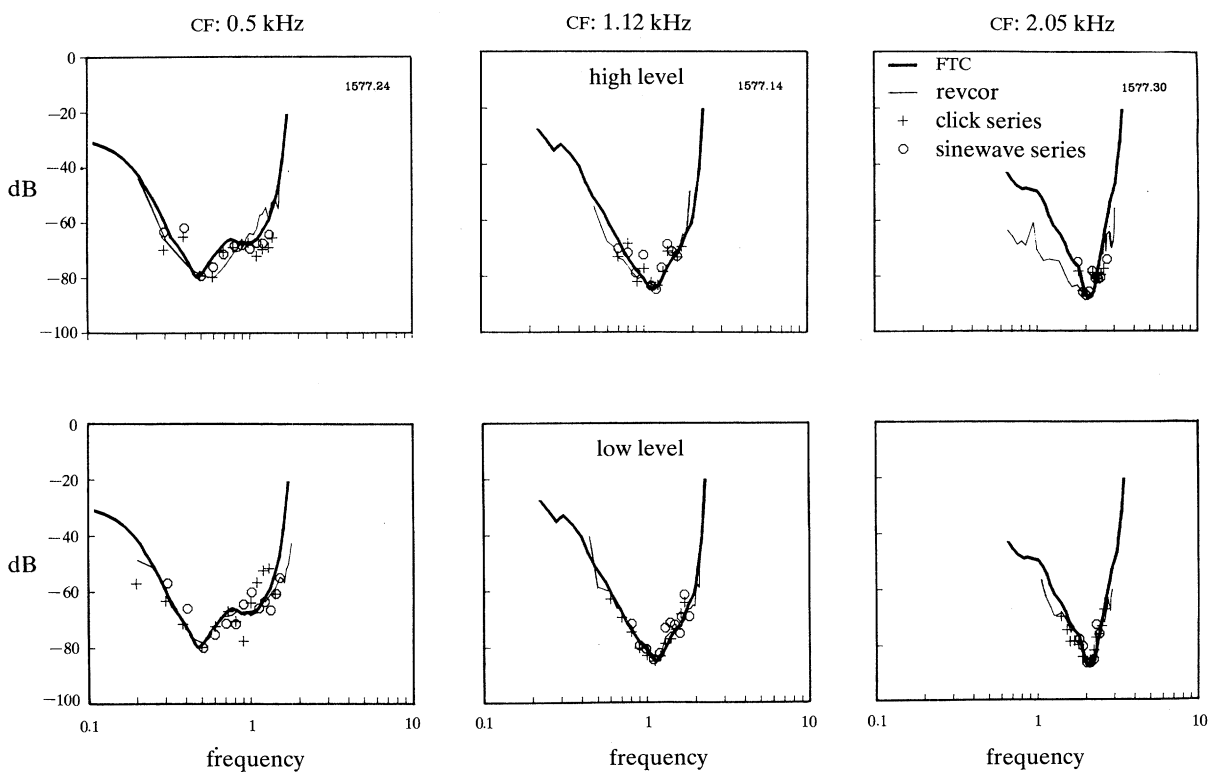

Figure 5. Derivations of cochlear filtering through the discharge patterns of cat cochlear nerve fibres of low, middle and higher characteristic frequency near threshold (lower half) and at stimulus levels 50 dB or more above threshold (upper half). Thick lines: pure tone frequency threshold curves; thin lines: filter functions derived from reverse correlograms with broad-band noise stimulation; crosses and circles: filter functions derived from weighting measures from temporal synchrony in response to click trains and sine-phase mixed tone complexes, respectively. (From Evans 1989*a*.)

noise (thin line). (In the case of broadband noise, the filtering was extracted by the reverse correlation technique of De Boer (1969); see Evans 1977, 1985*a*). Superimposed is the pure tone FTC (thick line). The filtering remains amazingly well preserved in the weighting of the time pattern over a surprisingly large dynamic range: as great as 90 dB in the cat (Evans 1977, 1981). (In the guinea-pig, however, there is evidence from our own and other studies that there are greater nonlinearities with level (Harrison & Evans 1982; Cooper & Evans 1988), as appears also to be the case in the rat (Moller 1977).)

One question which has been of great interest is how important these temporal patterns of spike discharge are for the determination of pitch. There has been much debate over the years as to which of the 'place' or 'time' neural representations is most relevant. My own studies of attempts by others to disprove the importance of time cues in pitch perception have led on the one hand to a realisation of the importance of cochlear tuning in the determination of the temporal patterns of spike discharges and on the other, to the position that it seems inescapable that both place and time cues must be involved in the perception of pitch independently or together, each assuming different importance depending upon the stimulus. Figure 6*a* shows stimuli (originally devised by Patterson (1973)) but used by Wightman & Green (1974) to test the importance of time cues in pitch perception. The two stimuli in figure 6*a* are the waveforms generated by summing the fifth to the tenth harmonics of a 200 Hz fundamental mixed in cosine phase (left) and random phase (right). The former waveform is very periodic, the other aperiodic. Wightman & Green argued that the cosine-mixed waveform could be expected to produce highly synchronized discharges in cochlear fibres by virtue of the waveform periodicity; the other not so. And yet the pitches and pitch strengths evoked by the two stimuli are virtually identical. Wightman & Green therefore argued that time cues were not likely to be involved in the perception of the pitch. However, the argument entirely ignored the role of cochlear filtering. If the two waveforms are passed through a cochlear-like filter, one gets the waveforms shown in figure 6*b*. Not surprisingly, the temporal discharge patterns of cochlear nerve fibres evoked by the very different stimulus waveforms of the upper row are virtually identical. In figure 6*c* are shown inter-spike interval histograms obtained from a single cochlear nerve fibre having a CF at the centre frequency of the harmonic complex under stimulation with the cosine- and random-phase mixed harmonics, respectively. This also demonstrates how even temporal representations of aspects of complex sounds are determined by the peripheral filtering mechanisms, and are therefore importantly correlated with the place of origin.

I have not found a pitch-evoking stimulus where the pitch heard could not be predicted from the fine-time structure of the cochlear nerve fibre discharges as seen in the inter-spike interval histogram or autocorrelogram analyses of the discharge patterns of cochlear fibres in the dominant region of CFS (Evans 1978*a*, 1983, 1986, 1989*b*,*c*). I have long gone on record that the brain is likely to use both place and time cues for pitch: either will suffice; but when both are present and congruent, then the most salient and discriminable pitch will be heard (Evans 1978*a*; 1989*c*).

3. SPECTRAL AND TEMPORAL CONTRAST ENHANCEMENT: THE COCHLEAR NUCLEUS LEVEL

It is at this level that the cochlear nerve input diverges

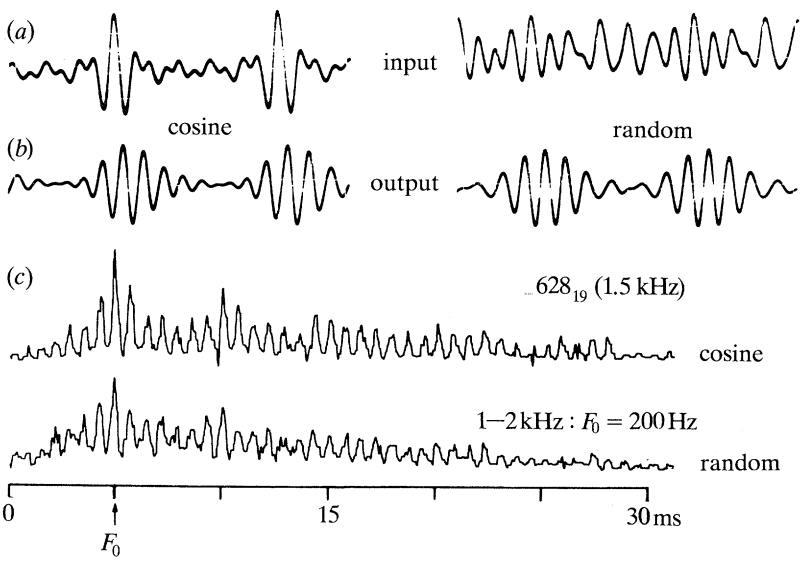

Figure 6. Phase effects are minimised by cochlear filtering. The waveforms in (*a*) represent the result of summing the fifth to the tenth harmonics of a common fundamental in cosine (left) and random phase (right) respectively. (*b*) Effect of filtering the above signals by a band-pass filter with half power bandwidth approximately equal to neural bandwidths of appropriate frequency. (*c*) Inter-spike interval histograms of a single cochlear nerve fibre in response to the signals in (*a*), in which the harmonics are evenly distributed across the cochlear fibre's filter function (CF: 1.5 kHz); fundamental frequency of complex: 200 Hz. (From Evans 1978*a*.)

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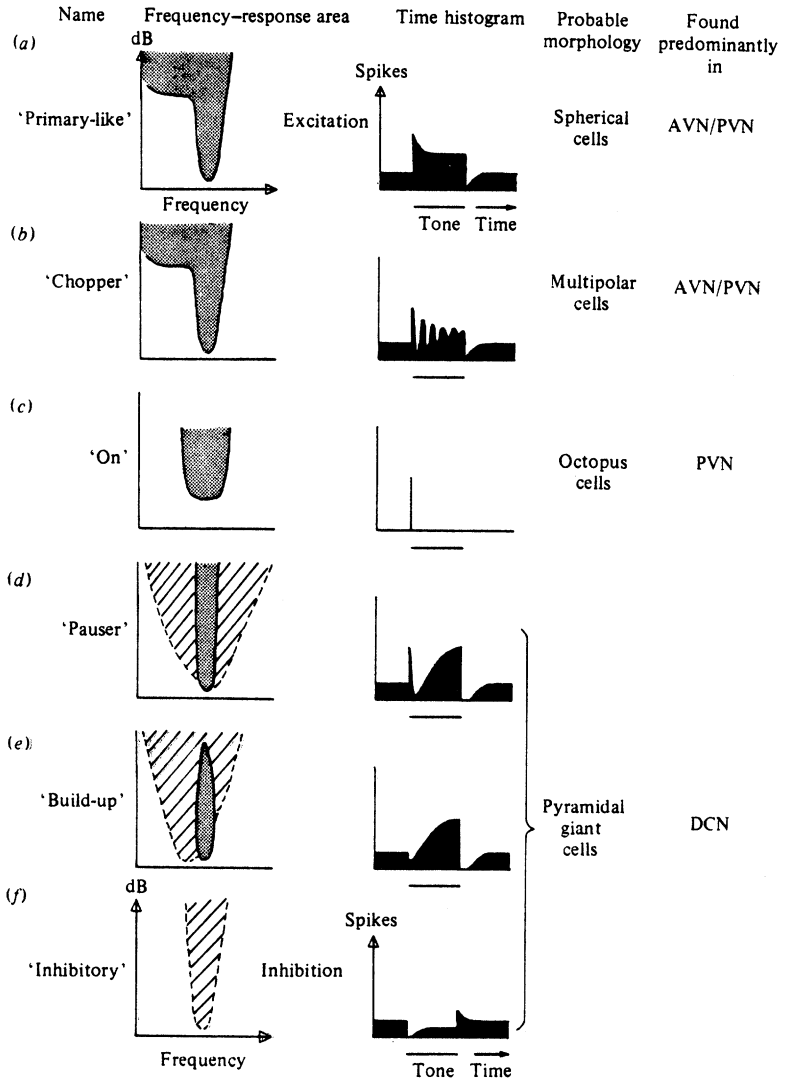

Figure 7. Diagram of frequency and time responses of major types of cells in cochlear nucleus. Left-hand column: diagrams of frequency response areas (axes as in (*f*)) indicating typical excitatory (stippled) and inhibitory (shaded) frequency-response areas of each type of cell. Inhibition alone (*f*) or inhibition combined with excitation (*d*, *e*) is found predominantly in the morphologically more complex dorsal cochlear nucleus (DCN). Middle column: schematic diagrams of peristimulus-time histograms of response to characteristic frequency tone of each type of cell (axes as in (*f*). The shape of the PST histogram gives rise to the 'nick-name' of each cell type to the left of the left hand column. Right-hand column: probable cell types and location. (From Evans 1982.)

to innervate a wide variety of types of cell (see diagrammatical and simplified representation in figure 7) in terms of location, morphology, receptive field organisation and response as a function of time before, during and following stimulation (see Evans (1975*a*) and Young (1985) for reviews).

A great deal of interest has centred on the class of cells found in the dorsal division of the cochlear nucleus (DCN) that exhibit extensive lateral inhibition of their response at frequencies above and below a narrow or barely present excitatory area: the type IV cells of Evans & Nelson (1973), and Young and colleagues (e.g. Young 1985), and figure 7*e*.

What is the function of this lateral inhibition? In recent experiments (Zhao & Evans 1990; Evans & Zhao 1992*a*), we have been able to demonstrate that this lateral inhibition is glycinergic: comparing the responses before and after blockage by the glycine antagonist, strychnine, allows us to dissect out the contribution made by the inhibition (figure 8). In figure 8*a* are the automatically mapped receptive fields of a type IV cell in the guinea-pig cochlear nucleus. The two left-hand maps indicate in the height of the small bars, the spike count in response to a tone burst of different (randomized) frequencies and levels indicated by the centre of each bar. The left-hand map is the control, and shows, in the 'white' patches, the lateral inhibition, surrounding barely discernable patches of excitation (between 11 and 12 kHz). Blocking the inhibition with strychnine (middle column) reveals the true extent of the excitatory input to the cell. By subtraction of these receptive fields, we can also derive the extent of the inhibitory field, as shown in the 'three-dimensional' contour plot on the right. It extends throughout the excitatory receptive field, and in fact is strongest at the excitatory

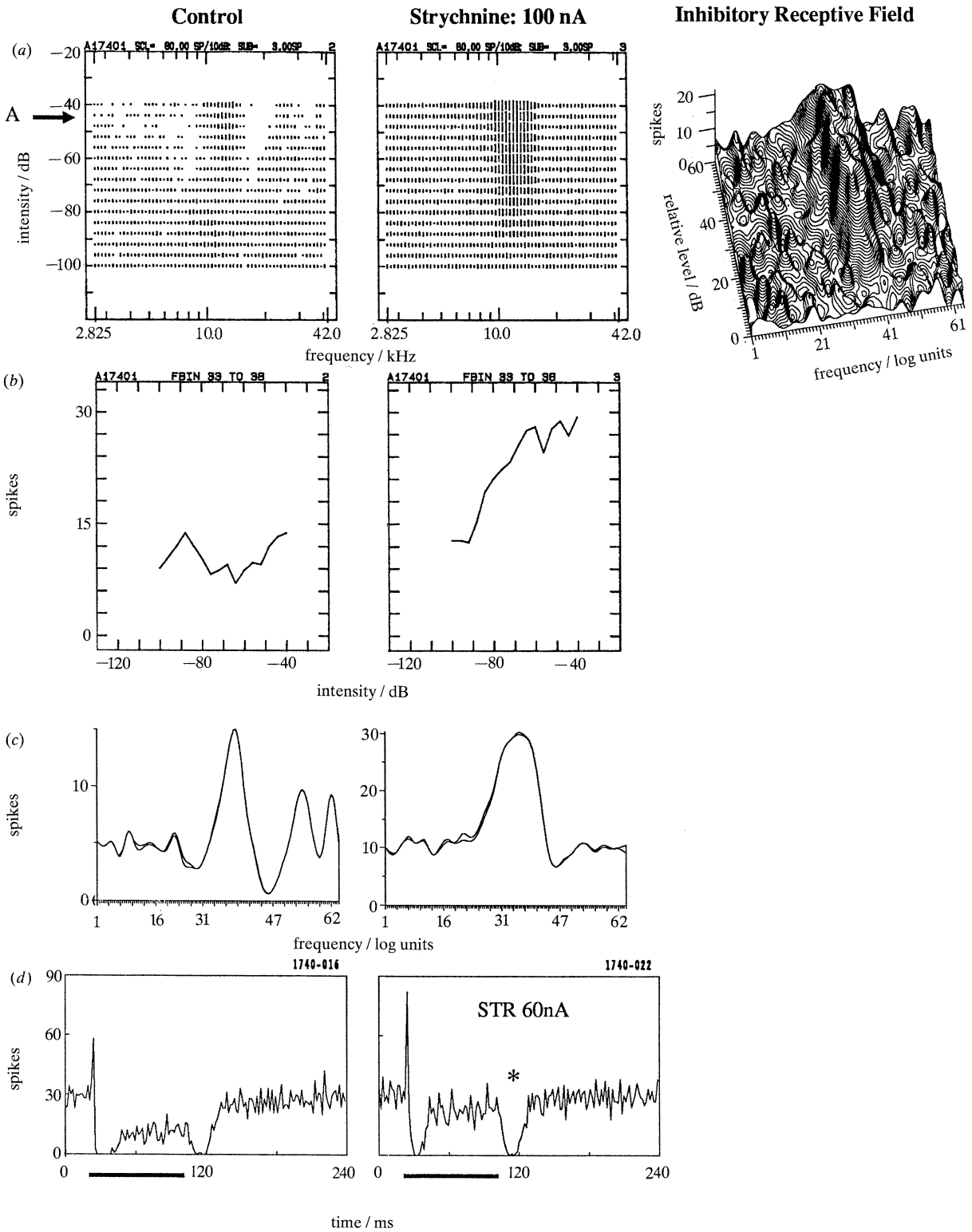

Figure 8. Role of 'lateral' inhibition in determining the response properties of dorsal cochlear nucleus (type IV) cells. Left-hand column shows control analyses; middle and right-hand columns show identical analyses after blocking the inhibition by the iontophoretic application of 100 nA strychnine. (*a*) Receptive field maps; (right) three-dimensional contour map of the strychnine-blocked inhibition, obtained by subtracting the control receptive field map from that obtained under strychnine. (*b*) Rate-level functions obtained at CF (12 kHz), from the receptive field maps in (*a*). Note conversion by strychnine blockade of non-monotonic rate-level function (control) into a steep monotonic function. (*c*) Iso-level functions taken at 50 dB above threshold (−44 dB) indicated by the arrow A in (*a*). Note extensive inhibitory side-bands in control case, surrounding narrowed excitatory response region, and removed by the strychnine blockade (right) with widening of the excitatory area and reduction in response contrasts. (*d*) Peristimulus-time histograms of the cell at 8 kHz, i.e. in the inhibitory side-band below CF. Note strychnine blockade of the sustained inhibition only, leaving unaffected the transient inhibition at the on-set of the stimulus, and off-inhibition (indicated by asterisk). Bar indicates tone. (From Evans & Zhao 1992*c*.)

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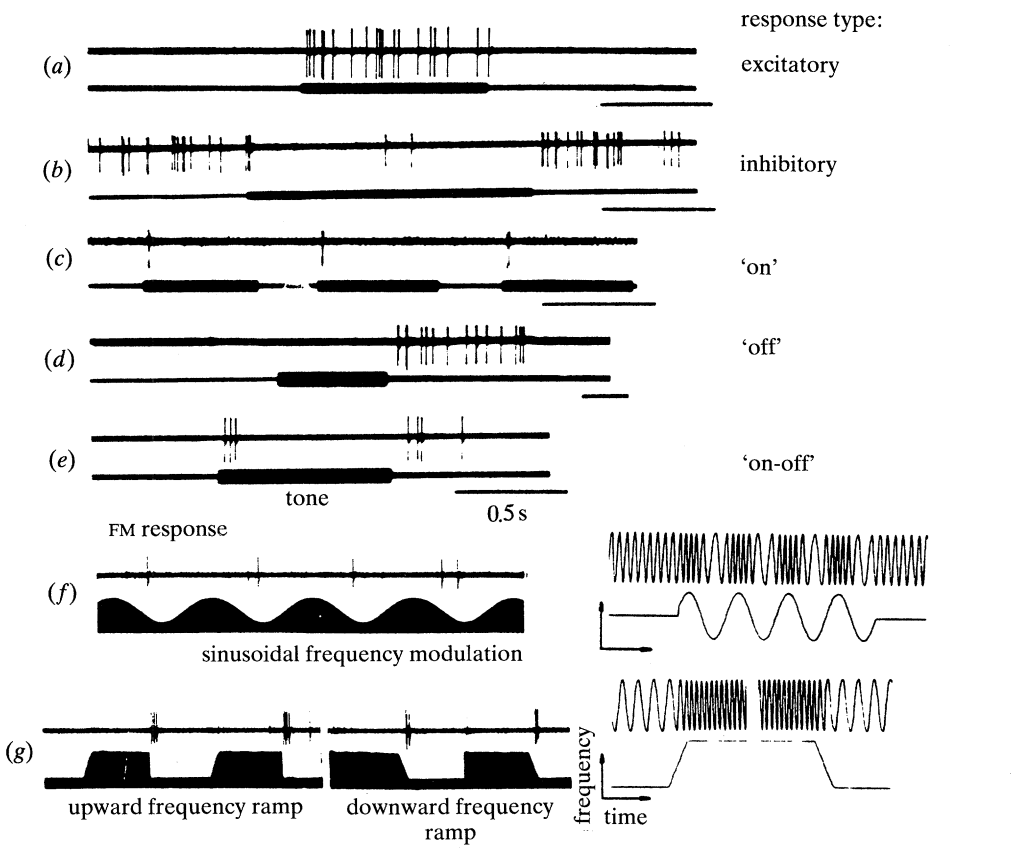

Figure 9. Variety of response types of cells in primary auditory cortex. (*a–e*) Types of response to steady tones. (*f*, *g*) Cell responding to frequency-modulated, not steady tones. Note response selectivity to direction of frequency sweep: in the downward direction, not to upward sweeps. Black envelope indicates excursions of frequencies illustrated by the waveforms to the right. (From Evans 1968, 1982.)

CF. (Thus, the term *lateral* inhibition is misleading.) Figure 8*b* shows the rate-level functions at the CF. Strychnine blockade of the inhibition converts the non-monotonic rate-level function characteristic of type IV cells into a monotonic function (right-hand plot) characteristic of primary afferents. Figure 8*c* shows the corresponding iso-level functions, i.e. response as a function of frequency at the constant level indicated by the arrow at A in figure 8*a*. In the control case (left plot), inhibitory 'troughs' surround the narrow excitatory response centre. Strychnine blockade of the inhibition (right-hand plot) eliminates the inhibitory troughs and reveals the true width of the excitatory receptive field. Thus, we can see that the 'lateral' inhibition is responsible for narrowing the excitatory response area and enhancing spectral contrasts. Young (this symposium) will show extreme examples of this function in connection with his hypothesis that the DCN is concerned with the analysis of the sharp spectral notches generated by reflections within the pinna. As we have shown elsewhere (Palmer & Evans 1982), 'lateral' inhibition can also bias a cell's 'working-point' to extend and optimize its dynamic range.

But not only spectral contrasts but temporal contrasts are further enhanced at the cochlear nucleus level. Off-inhibition (the suppression of discharge immediately following the offset of a stimulus, whether excitatory or, as in figure 8*d*, inhibitory) serves to enhance the response contrast between the stimulus 'on' and the stimulus 'off'. (As yet, we have not been able to determine what transmitter, if any, is responsible: strychnine blockade leaves the off-inhibition unaffected as shown at the asterix.) This enhancement of temporal contrast improves the modulation of discharge of cochlear nucleus cells in response to amplitude modulated stimuli, compared with cochlear nerve fibres, as was first shown by Moller (1972).

We have recently shown that there are several different types of inhibition in the cochlear nucleus, responsible for different aspects of spectral and temporal contrast enhancement, each apparently under control of different neurotransmitter systems and therefore capable in principle of exquisitely fine control by other parts of the auditory system (Evans & Zhao 1992*b*,*c*).

4. ABSTRACTION OF SALIENT FEATURES OF COMPLEX STIMULI: AUDITORY CORTEX

Compared with the cochlear nerve and even the cochlear nucleus where responses are relatively straight-forward representations of stimulus spectral content, the responses obtained at the level of the auditory cortex are a very mixed bag (figure 9). 'On' responses, inhibitory responses, 'off', 'on–off' responses are very common to pure tone stimuli. Even in the primary auditory cortex of the unanaesthetised preparation the cells are difficult to drive reliably by pure

tones. Many cells respond much more vigorously and consistently to complex sounds. In the case of the cat, the most effective stimuli (used as typical 'search stimuli') are what I have termed 'backdoor noises': the sounds that are heard outside the average British backdoor around midnight calling the pet feline in for the night: kissing, hissing noises, jangling of keys, etc. (Evans 1968)!

Of particular interest for complex signal analysis, are the small minority of cells that do not respond to pure tones at all, but do respond selectively to complex patternings of frequency and amplitude in time (figure 9*f*,*g*). Thus, there are cells specifically selective to frequency changes which are capable of signalling both the direction (e.g. to downward frequency transitions in the single cell illustrated in figure 9*f*,*g*) and the rate of frequency change. These were first described by Bogdanski & Galambos (1960) but independently and in more detail by Evans & Whitfield (1964), Whitfield & Evans (1965); and by Suga (1964).

Cells in the uppermost levels of the auditory system are therefore capable of extracting or abstracting salient features of a complex stimulus: is it on, is it off, has it just turned on or off? Is the frequency changing, if so in what direction, at what rate? And so on.

These findings have been extended beautifully in the discovery of cortical cells selective in their response to features of species-specific vocalizations: by the late Peter Winter and colleagues (e.g. Winter & Funkenstein 1971) in the squirrel monkey, and by Suga (this symposium) in the bat.

5. EPILOGUE

None of these considerations that this volume addresses are of purely academic interest. Some of us have interests in developing neural prostheses for restoring some form of hearing to the profoundly hearing impaired, for example with multi-channel cochlear implants (see Evans (1985*b*) for review). We need detailed knowledge on the way in which complex sounds are encoded in the auditory periphery, so that we may mimic these patterns as accurately as feasible, by artificial, electrical, stimulation of the auditory periphery either at cochlear or brainstem levels. Currently, this artificial stimulation is subject to severe technological limitations, particularly at the electrode-biological interface. It is equally important therefore to know how the central levels of the auditory system might deal with this imperfectly as well as with normally encoded information.

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