

Proceedings of The Institute of Acoustics

AUDITORY CODING AND THE PERCEPTION OF STIMULI.

I. C. WHITFIELD

Neurocommunications Research Unit, University of Birmingham

One of the ultimate objects of the study of Neurocommunications is to establish a relationship between the way information is coded in neural pathways and the way stimuli are perceived. Perhaps more progress has been made in the solution of this problem in the auditory system than in other sensory pathways and if a complete solution is still far off we can at least begin to point the way.

We may start by asking the question -- "Why do we think of complex tones in terms of a fundamental and its overtones?" We may end with the question -- "Why do we perceive the world as a set of objects?" It was Ohm (5) who first proposed a Law of Auditory Analysis based on the then recently formulated Theorem of Fourier. Although the purely mechanical analytic mechanisms put forward at that time have proved to be untenable, nevertheless it has since been confirmed that the combined effect of a rather crude mechanical frequency separation in the cochlear partition, followed by a (not yet well understood) sharpening process at the receptor level does result in a pattern of activity in the auditory array that will in turn provide at the lemniscal level a pattern of activity which represents rather closely the terms of the Fourier Series corresponding to the complex stimulus. An immediate difficulty is that we cannot have either individual fibres or discrete fibre groups representing by their discharge rate the amplitude coefficients of individual Fourier terms. Because of the shape of individual fibre response curves, a given stimulus frequency will excite a large group of fibres, the majority of which will also be excited by an adjacent, but discriminable, stimulus frequency. Indeed, the jnd for frequency depends, on this basis, on the detection of some liminal shift in the fibres at the edge of the active block (7). In the case of a single tone that change can be calculated to be of the order of 50 fibres (9). Because, too, the shape of the fibre response curves is roughly triangular, the number of fibres excited by a tone increases with stimulus intensity, and there will be a similar 'edge change' (which turns out to be of about the same magnitude - 50 fibres) for the jnd of intensity. Because of the comparatively small dynamic range, fibre discharge rate does not appear to be a very important variable in coding intensity. This is especially true within the brain-stem itself, because the transfer function associated with the cochlear nucleus emphasises the 'on-off' nature of the individual fibre responses (7).

The slopes of the fibre response curves determine the shift in the active array with frequency, and are hence related to frequency discrimination. The widths of the response curves (and of the active array) are likewise related to frequency resolution, but do not wholly determine it. Simple theory would suggest that resolution ought to deteriorate rapidly with increasing intensity -- a deduction not in accord with the facts. However that simple theory leaves out of account both lateral inhibition in the cochlear nucleus, and perhaps more important, the role of the centrifugal pathways. Centrifugal terminals in the cochlear nucleus have an important function in delimiting the critical band (6),

Proceedings of The Institute of Acoustics

Auditory coding and the perception of stimuli.

and it is possible that the olivo-cochlear bundle plays a similar role at the periphery (2,9). The overall result of these various mechanisms is to produce groups of active fibres within the lemniscal array whose positions in the array correspond to the terms of the Fourier Series representing the complex tone, and where the number of fibres active in each group represents the coefficient (amplitude) of that term. This pattern therefore forms a basis for our ability to 'listen to' the separate overtones of a complex sound. It also suggests why, if we listen to an acoustic square wave, and change the mark/space ratio from unity to [say] five-to-one, we are not aware of a change in the mark/space ratio as such; what we do hear is the entry of the second harmonic, corresponding to the appearance of the second term in the Fourier Series (the 'unity' waveform comprises, of course, only the odd terms).

Another transformation we might look at is that arising in the medial superior olive. Here a code based on the relative timing of impulses from the two ears is transformed into a code dependent on the ratio of the activities in the ascending pathways on the two sides (3). Since a sound wave from a source on, say, the left will clearly arrive at that ear before it arrives at the right ear, the relative brain-stem activity clearly encodes the side of the signal. Let us leave this point for the moment and return to the complex tone.

Although it is relatively easy with a little practice to listen to individual harmonics of a complex tone, nevertheless naively the attributes of such a tone are timbre and pitch. A different set of harmonics of the same series will in general have the same pitch, though a different timbre. Indeed, a suitable anharmonic series may also have a pitch identifiable with a harmonic series (8). A normal cat hears a tone complex $4f + 5f + 6f$ as having a pitch equivalent to a single tone of frequency f (4). However, after bilateral removal of auditory cortex, although the animal is capable of responding to the simple tone f , it no longer treats the complex $4f + 5f + 6f$ as equivalent, although it can be trained anew to respond to the elements of the complex. It appears that the constancy of pitch across different sets of related harmonics is a cortical phenomenon; the decorticate animal treats each harmonic set as distinct. Frequency discrimination is as good in the decorticate as in the intact animal; pitch constancy is lost.

An exactly analogous situation exists in the phenomena associated with sound localization. If a decorticate cat listens to trains of dichotically presented click pairs, it readily learns to distinguish the situation right-ear-leading from left-ear-leading (1), employing presumably the mechanism previously discussed. Such a cat can also learn to respond when a single train of clicks in the right ear changes to a similar train in the left ear. However, it has to learn each of these as a separate problem, whereas the intact animal, having learnt one, transfers immediately to the other. A clue to this difference is provided by the observation that animals (several species) deprived of auditory cortex can 'tell' whether a sound is on the right or the left, but nevertheless cannot approach the sound -- i.e. localize it as an external source. Likewise with 'precedence effect' stimuli (13), the undecorticate animal can, at least in some cases, 'get the side right', but cannot determine the location of the

herein decorticate means without auditory cortex

Proceedings of The Institute of Acoustics

Auditory coding and the perception of stimuli.

source on that side (11).

The brain-stem transformations are analytic -- for example complex tones are transformed to a harmonic series. As a result we are aware of these analytic features, and animals can be trained to respond to the differences in the resulting neural patterns. However, each problem must be learnt separately. The corresponding cortical transformations appear to be synthetic. The corticate animal can concern itself with the similarities between related stimuli, as well as the differences between less closely related ones. We are concerned then with constancies -- the constancies of size, shape, position, that result in the perception of a stable external world even when the particular stimulus situation changes.

For some twenty years past, much effort has been put into the study of the sensory cortex as a 'feature detector', that is to say an extractor of progressively more elaborate features of an object, such as direction of movement, orientation, angular relationship. There are many reasons why such a hierarchical view both of perception and of cortical synthesis is inadequate (12). Conceptually it appears to demand an infinite regression, and practically it fails abysmally, for example, to account for the results of cortical ablation. As I have tried to make clear, what is lost in cortical damage is not the response to some particular feature of the stimulus -- that can usually be recovered. What is lost is the set of constancies with which we normally view the world (10). For the intact animal each new stimulus situation is not entirely separate. Pitch can remain constant over considerable changes in harmonic structure; the position of a sound source is distinct from the sound being emitted. In general, these factors give an externality to the way we hear and see the world about us. Just as we think in terms of the harmonic structure of sound because of the nature of its corresponding brain-stem transform, so, I suggest, the constancies of e.g. pitch and location must have their basis in the particular nature of the cortical transform. Neither feature detection nor 'tonotopicity' appear even to be starters in the candidacy for a suitable transformation. The transform must be distributive to fulfil the conditions and must not put severe constraints on the neuronal elements. Such a transform might plausibly be anatomically represented as a matrix.

References

- (1) S. AXELROD and I.T. DIAMOND 1965 J. comp. physiol. Psychol. 59, 79-89. Effects of auditory cortex ablation on ability to discriminate between stimuli presented at the two ears.
- (2) J.H. DEWSON 1968 J. Neurophysiol. 31, 122-130. Efferent olivo-cochlear bundle: some relationships to stimulus discrimination in noise.
- (3) J.L. MALL 1964 Tech. Rpt. 416. Research Lab. of Electronics (M.I.T. Cambridge, Mass.) Binaural interaction in the accessory olivary nucleus of the cat.
- (4) H.H. HEFFNER and I.C. WHITFIELD 1976 J. acoust. Soc. Am. 59, 915-919. Perception of the missing fundamental by cats.

Proceedings of The Institute of Acoustics

Auditory coding and the perception of stimuli.

- (5) G.S. OHM 1843 Ann. d. Phys. 59, 497-565. Ueber die Definition des Tones, nebst daran geknüpfter Theorie der Sirene und ähnlicher tonbildender Vorrichtungen.
 - (6) J.O. PICKLES 1976 J. Neurophysiol. 39, 394-400. Role of centrifugal pathways to the cochlear nucleus in determination of critical bandwidth.
 - (7) I.C. WHITFIELD 1957 Progress in Biophysics and Biophysical Chemistry 8, ed. Butler & Katz, 2-47. Pergamon, London. The physiology of hearing.
 - (8) I.C. WHITFIELD 1970 Excitatory Synaptic Mechanisms ed. Andersen & Jansen, Universitets forlaget, Oslo. 277-285. Neural integration and pitch perception.
 - (9) I.C. WHITFIELD 1978 Handbook of Perception vol 4, ed. Carterette & Friedman, 163-186. Academic Press, New York, The neural code.
 - (10) I.C. WHITFIELD 1978 Brain Behav. Evol. 15, The object of the sensory cortex.
 - (11) I.C. WHITFIELD 1979 J. Physiol. 288, 105P. Auditory cortical lesions and the precedence effect in a four-choice situation.
 - (12) I.C. WHITFIELD 1979 Contributions to Sensory Physiology vol 6, ed. Neff, Academic Press, New York. Coding in the auditory cortex.
 - (13) I.C. WHITFIELD, J. CRANFORD, R. RAVIZZA and I.T. DIAMOND 1972 J. Neurophysiol. 35, 718-731. Effects of unilateral ablation of auditory cortex in cat on complex sound localization.
- I.C. WHITFIELD, I.T. DIAMOND, K. CHIVERALLS and T.G. WILLIAMSON 1978 Expl. Brain Res. 31, 221-234. Some further observations on the effects of unilateral cortical ablation on sound localization in the cat.