

## SPECTRO-TEMPORAL CHARACTERIZATION OF AUDITORY NEURONS: REDUNDANT OR NECESSARY?

J.J. EGGERMONT, A.M.H.J. AERTSEN, D.J. HERMES and P.I.M. JOHANNESMA

*Laboratory of Medical Physics and Biophysics, University of Nijmegen, Nijmegen, The Netherlands*

(Received 28 January 1980; accepted 18 February)

For neurons in the auditory midbrain of the grass frog the use of a combined spectro-temporal characterization has been evaluated against the separate characterizations of frequency-sensitivity and temporal response properties. By factoring the joint density function of stimulus intensity,  $I(f, t)$ , preceding a spike, into two marginal density functions  $I_1(f)$  and  $I_2(t)$  one may under the assumption of statistical independence reconstruct the joint density by multiplication:  $I_1(f) \cdot I_2(t)$ . The reconstructed  $\hat{I}(f, t)$  is compared to the original  $I(f, t)$  for 83 neurons: in 23% thereof the  $\hat{I}(f, t)$  appeared to be vastly different from  $I(f, t)$ . These units appeared to be located dominantly in the ventral parts of the auditory midbrain and had a latency exceeding 30 ms. On the basis of the action-potential wave forms the absence of non-separable  $I(f, t)$  in the incoming nerve fiber population is concluded. A spectro-temporal characterization of auditory neurons seems mandatory for investigations in and central from the auditory midbrain.

Key words: second-order cross-correlation; neural convergence; frog; auditory midbrain, spectro-temporal properties.

### INTRODUCTION

Auditory nerve fibers and cells generally are characterized on the basis of tuning curves, spike rate–intensity functions and PSTHs to clicks and tones at the CF [17]. From these measurements a parametrization into CF,  $Q_{10\text{dB}}$ , latency, firing rate and adaptation-time constant serves a further data reduction. These parameters are not independent and relations have been derived for the auditory nerve that relate tuning and timing properties [14].

Other measures for frequency selectivity such as iso-intensity rate functions relating firing rate and stimulus frequency have been in use besides period histograms from which latency as well as lock to the phase of the stimulus may be derived [3,23]. In all cases, however, spectral and temporal properties of the stimulus–response relationship are treated as independent phenomena that can be studied separately. This approach appears to be justified for neurons in the auditory nerve where on basis of tuning and timing properties one may predict the response of the neuron to a variety of stimuli ranging from simple tones to complex sounds [9]. However, there is some evidence that this is no longer so for more central parts of the auditory system [5,24].

Since for narrowly tuned neurons the influence of stimulus frequency is related – especially in iso-intensity contours – to excitation level, one may find latency values

which are highly frequency dependent [18]. So, in general there are no a priori arguments, even for the peripheral part of the auditory system, to expect that the spectro-temporal sensitivity of auditory neurons is separable into two independent dimensions: frequency and time properties. Central auditory structures in addition are considered to be more and more tuned to biological information-bearing elements [25], such as features of species-specific vocalisations. These natural sounds possess an intricate spectro-temporal structure, and to visualize this better than just a representation of signal waveform would do, a combined spectrotemporal representation, the sonogram, has come into use [21].

Classical stimulus–response relations are based on spike rate or on just-detectable changes in spike rate which serve to plot dimensions of the stimulus against each other, e.g. intensity vs. frequency, to give a tuning curve. Stimuli which are fully controlled (i.e., deterministic) are presented repeatedly in order to arrive at reasonable estimates of tuning and timing properties. Statistical procedures, in contrast, investigate the stimulus–response relationship by observing functionals of the stimulus whose presence causes – and therefore precedes – a spike. Averaging these functionals (e.g. stimulus amplitude, -intensity, -envelope) is formally equivalent to cross-correlation between spikes and stimulus functionals. By taking as the stimulus wide-band Gaussian noise and as the functional its signal values, one arrives at an estimate of the neurons linear response properties. When the system is nearly linear this approximates the impulse response for the neuron [6,7,11,19,26]. This function comprises the temporal aspects of the neurons response properties, it offers an estimate of the latency and predicts click PSTHs, it also comprises the spectral or tuning aspects of the neuron, these are elucidated by Fourier transformation. Although the determination of spectral and temporal neural properties in this case can be done on basis of one and the same stimulus, both characteristic dimensions are still uncoupled and generally studied separately.

When there is a lack of phase lock [15] one needs higher order cross-correlations or correlation between spike and stimulus intensity, and a transformation of timing properties into tuning properties is no longer straightforward [16]. Tonal stimuli, when used in the classical approach, are characterized by frequency, duration, intensity, envelope, and amount of FM or AM. By introducing a complex representation of stimuli [1] a combined spectro-temporal characterization can be given based on instantaneous frequency and instantaneous amplitude (or intensity). Correlation between spike occurrences and functionals of the preceding tonal stimuli leads to the IFT representation [2]. This is a three-dimensional display of the spectro-temporal characteristics of the neuron in which tonal frequency and time before a spike are intricately coupled. From this representation a number of parameters, such as best frequency, response time, spectral width, temporal width, etc., may be derived which relate to classical measures as CF, latency,  $Q_{10dB}$  and peak width in PSTHs. In a number of cases, however, parametrization leads to a loss of information regarding the properties of the neuron.

The need for a spectro-temporal approach in characterizing neural units has been investigated for 83 units recorded in the torus semicircularis, a homologue of the inferior colliculus of mammals, of the grass frog (*Rana temporaria*, L.).

## METHODS

### *Stimulation*

Tonal stimuli with envelope  $m(t) = c(t/\beta)^{\gamma-1} \exp(-t/\beta)$ ;  $t \geq 0$ ;  $\beta > 0$ ; with various duration parameters  $\beta$  and constant form parameter  $\gamma = 3$  have been used [1]. Frequency range was generally 4 octaves, either from 125–2000 or 250–4000 Hz depending on the frequency characteristics of the neuron; occasionally 100–3000 Hz was used. Frequency values were selected in random order from 255 values equidistant on log frequency scale (64 intervals per octave). The amplitude factor was either 127 values at equal linear intervals covering a range of 42 dB, apart from the dynamic range of the envelope of the individual  $\gamma$ -tones, or was kept at a constant value. This random type of stimulation has been used with much effect [10] in determining tuning curves and rate intensity functions. Duration of the  $\gamma$ -tones was either 16 or 48 ms obtained by adjusting  $\beta$  and truncation of  $m(t)$ , intervals between successive  $\gamma$ -tones range from 0 to 1 s. These values were selected according to the neuron's properties in order to assure a stationary response over the complete stimulus sequence. When a 1 s interval was used the amplitude factor was kept constant in order to reduce the duration of a complete stimulus sequence. In the case of 16 ms duration with zero interval, for example, the complete sequence consists of  $255 \times 127 = 32,385$   $\gamma$ -tones with a total duration of approximately  $8\frac{1}{2}$  min.

The tonal stimuli were generated by a Programmable Stimulus Generator (PSG) comprising a programmable frequency synthesizer (Rockland 5100), the output of which was amplitude modulated by two serial 12-bits multiplying DA-converters (Hybrid Systems DAC 316-12) under stimulus control of a PDP 11/10. The generated waveform was low-pass filtered before it was amplified and presented to the animal by two electrodynamic microphones (Sennheiser, MD 211N) coupled to the frog's tympanic membranes with a closed sound system. The sound pressure level was measured in situ with a half-inch condenser microphone (Brüel and Kjaer 4143) connected to the coupler (for details see [15]). The frequency response of the sound system was flat  $\pm 5$  dB for frequencies between 100 and 3 kHz, a range quite sufficient for studying the auditory system in the grass frog (e.g. [4]). The frequency responses of both sound systems were made equal within 2 dB for the range of interest. Identical stimuli were presented to both ears in all cases; the maximal sound intensity was 89 dB SPL.

### *Recording*

Neural activity was recorded using stainless-steel microelectrodes with approximately 15  $\mu\text{m}$  exposed tip and a 1 kHz impedance of 2–14  $\text{M}\Omega$ , the neural activity was amplified (Grass P 16), and action potentials, were transformed into unitary pulses by means of a level discriminator and fed into a data-acquisition system using a PDP 11/34, the timing of which was controlled by the same external clock as for the PSG providing a time resolution of 10  $\mu\text{s}$ .

### *Data analysis*

Spectro-temporal analysis of the stimulus response relation was performed by means of software and resulted in the average IFT-representation [2]: a function of two vari-

ables, frequency and time, from which several two-dimensional projections (by integrating over the third dimension) can be obtained. Among these, the IF-projection, constructed by integrating over the time window of interest, gives an estimate of the tuning properties of the neuron. The IT-projection is formed by integration over frequency either around CF or over all frequencies presented. The former situation leads to timing properties that will relate to those obtained from PSTHs of the response to tones at the CF; the latter could resemble the PSTHs of the responses to a noise burst. The formation and shape of these IF and IT properties from the IFT-representation are shown in Fig. 1A.

For a high-frequency sensitive neuron showing broad tuning with a frequency dependence in its latency which amounts up to 20 ms in a rather discontinuous way, the blackness of the representation indicates large intensity values. Shown is the average stimulus intensity as a function of frequency and time that precedes a spike. The time of occurrence of the spike is in the right-hand corner; the averaging is over a stimulus history of 128 ms in this case. The narrow vertical bar on the right represents the IF-projection, the neuron's tuning properties, showing a single best frequency at about 2000 Hz. The horizontal bar at the lower part of the figure represents the IT-projection, suggesting a maximum effect when the stimulus precedes a spike by about 35 ms. If one considers  $I(f, t)$ , the intensity as a function of two variables, as a joint density function (which may be justified after appropriate normalization), independence of both variables  $f$  and  $t$  requires that  $I(f, t) = I_1(f) \cdot I_2(t)$ , i.e., the product of two marginal density functions. In our case these are just the projections considered.

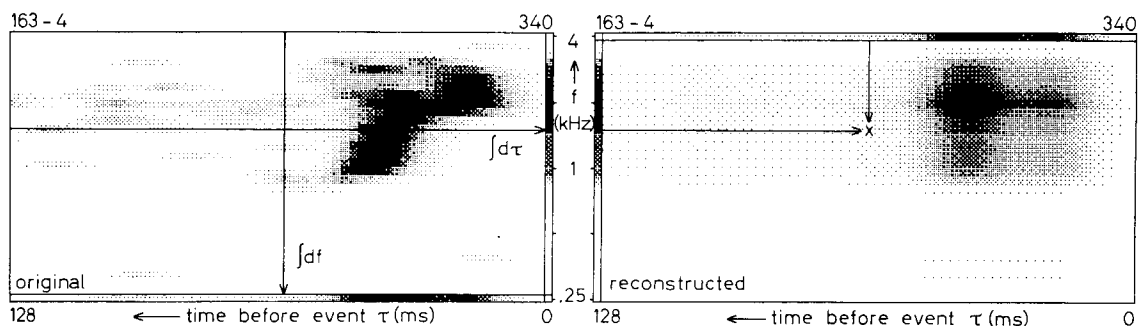


Fig. 1. Outline of the procedure. For a high-frequency unit (163-4) the spectro-temporal sensitivity is shown on the left. On the vertical axis stimulus frequency is displayed on a logarithmic scale, on the horizontal axis the time *before* a spike, running from right to left, is indicated. Increasing blackness indicates that more tones in that frequency–time domain on average preceded a spike than in frequency–time regions that are grey. White indicates that tones of this frequency–time combination did not produce a spike. One observes several black regions for different frequency–time combinations, suggesting multiple tuning. This feature is lost by integrating over time to obtain the frequency response as shown in the vertical bar on the right, indicating a single best frequency. Integrating over frequency produces the temporal intensity, horizontal bar at the lower part of the figure; the most black region suggests an average response time of 35 ms. In the right-hand side of the figure the *reconstructed* spectro-temporal sensitivity is obtained by multiplication of the spectral- and temporal sensitivity. The result is a single-tuned sensitivity with best frequency around 2 kHz and at the BF a relatively large temporal spread from 40 to 10 ms. The *reconstructed* picture – obtained under the assumption of independence of the spectral and temporal characterizations – clearly differs from the original.

From these two projections, one representing the neuron's spectral or tuning properties and the other its temporal or latency properties, one may *reconstruct* a combined spectro-temporal representation,  $\hat{I}(f, t)$ , under the assumption of *independence* of frequency and time properties. This is done by multiplying (Fig. 1B):  $I_1(f) \cdot I_2(t)$ . One observes a spectro-temporal representation that appears simply tuned but at the best frequency shows responses over a very wide time range.

If the reconstructed IFT is similar to the original one, the assumption of independence cannot be rejected, and obviously there was no necessity to use the combined spectro-temporal approach.

Independence of frequency and time properties assumes that latency is largely independent of stimulus frequency; some relatively simple dependence, however, will be neglected.

## RESULTS

For 83 neurons from the auditory midbrain of the frog a spectro-temporal characterization of the neural response properties has been given for tonal stimuli. In order to qualify for such a characterization based on a random-frequency, random-amplitude sequence of tones, the response rate over parts of the stimulus ensemble had to remain constant. Neurons, for instance, which ceased firing gradually during the presentation of a tonal sequence with 16-ms intervals could show quite stationary responses when the interval was lengthened to e.g. 112 ms or, in some cases, to 952 ms. As a consequence, the particular selection of the stimulus ensemble was based on stationarity of the response and, in addition, a sufficient production of spikes. Since firing rates in the midbrain of the frog are relatively low ( $<20/s$ ), a long stimulus sequence is generally needed. When presentation intervals were 1 s, the 16 ms tones were replaced by 48 ms tones, which did not greatly change the response characteristics except for some gain in spike yield.

Stationarity of the response to a given stimulus ensemble was assumed when the number of spikes in the second half of the stimulus ensemble was the same ( $\pm 10\%$ ) as in the first half of the stimulus. For stimulus ensembles consisting of a repetition of identical sequences the numbers of spikes to each sequence were compared. Therefore, a rather heuristic measure of stationarity was used and no efforts were made to calculate the moments of the distribution functions for the occurrence of the spikes.

The neuronal data were arranged according to the type of stimulation used and the combined spectro-temporal characterization was compared to the reconstructed one based on independence of spectral and temporal properties. The authors independently judged the similarity of both spectro-temporal characterizations and chose their own criteria. Among these were the preservation of Best Frequencies in the reconstruction, the preservation of spectral width (i.e., quality of tuning), and one of the more important criteria: the effect of loss of frequency-dependent latencies in double- or multiple-tuned neurons.

The use of a more objective method for judging differences between the original and reconstructed spectro-temporal receptive field (e.g. by pattern recognition methods such as used for classification of the spike wave forms, see legend of Fig. 3) was not considered appropriate at this stage of the investigation. Our judgements will therefore have been

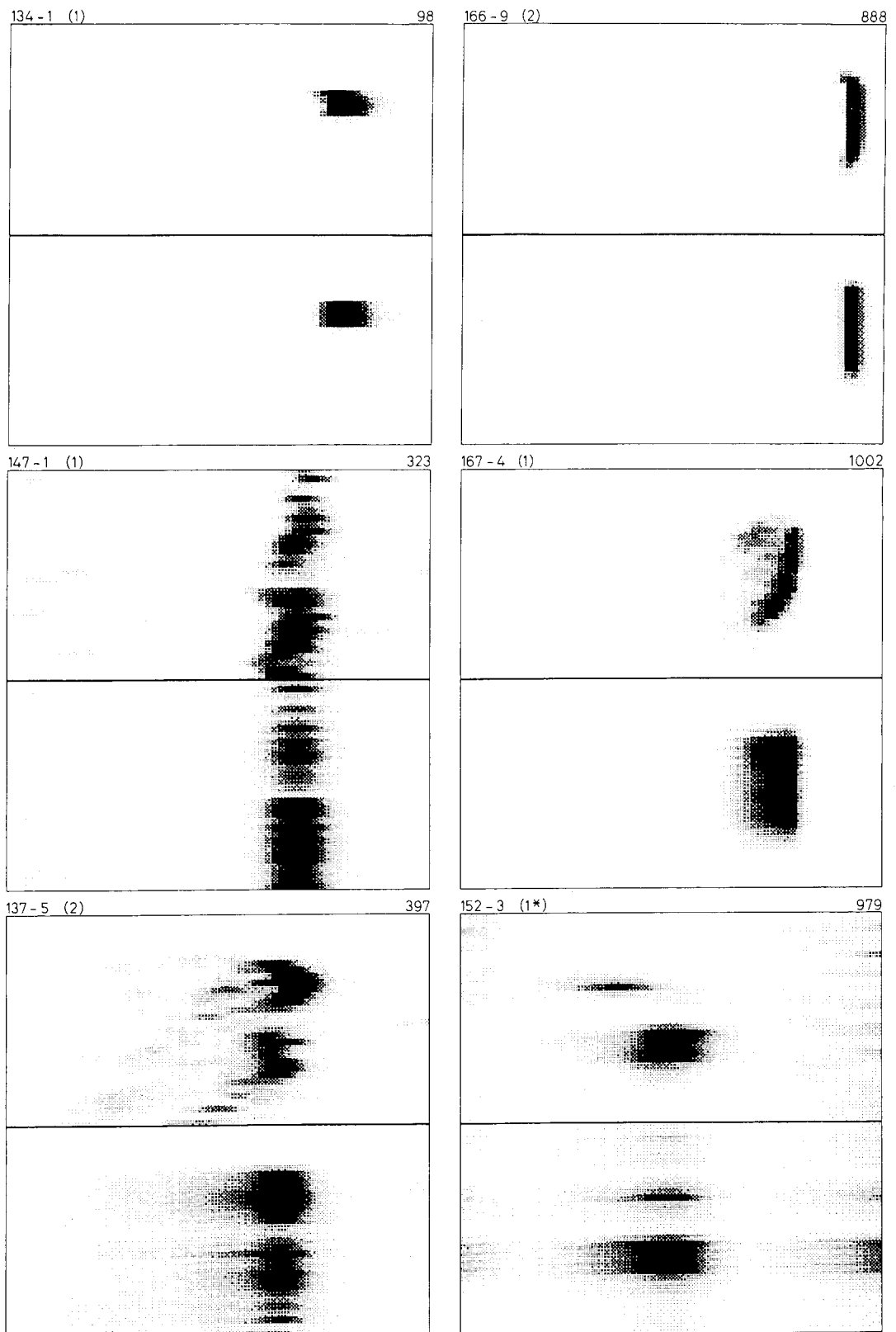
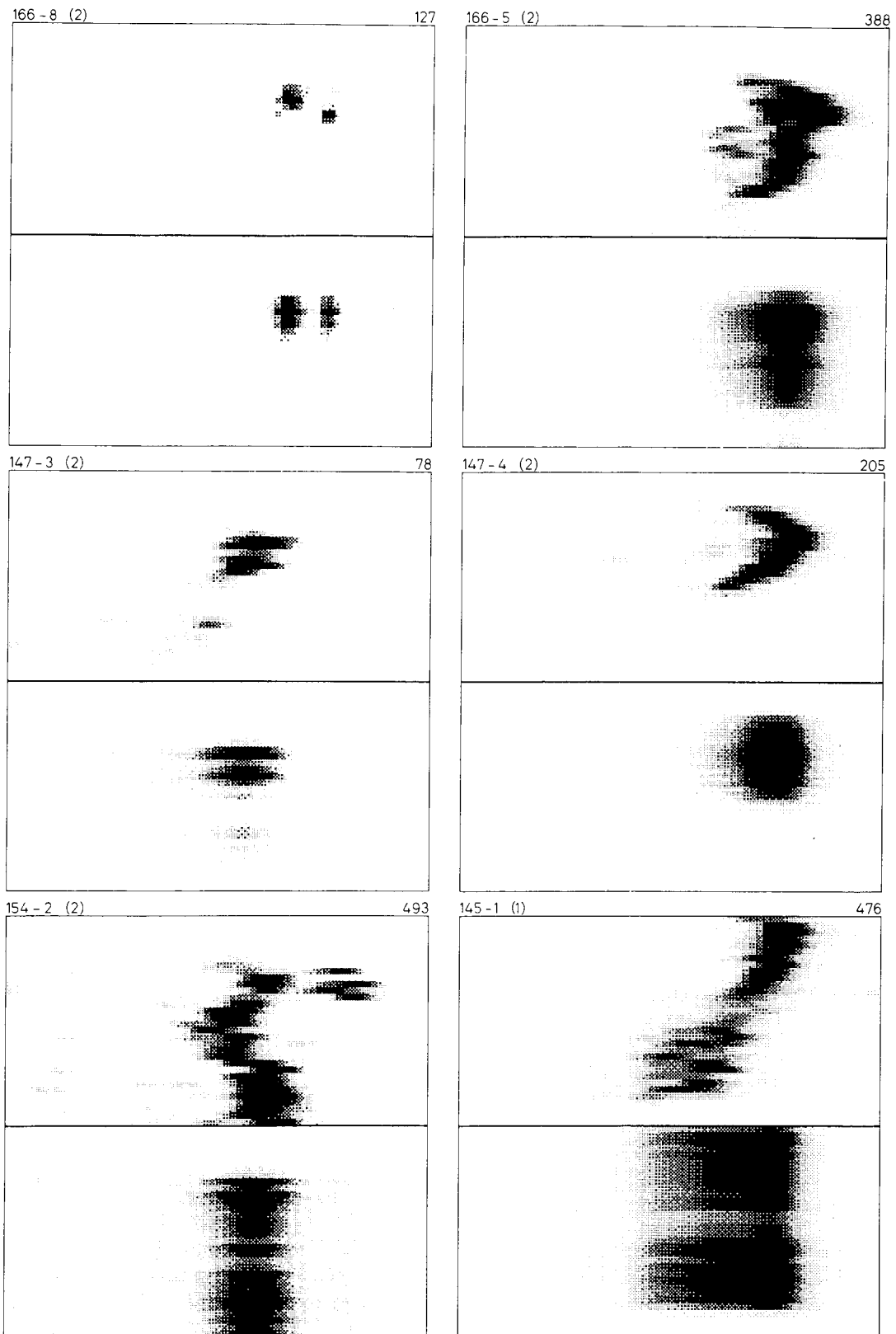


Fig. 2. (A) Original and reconstructed spectro-temporal sensitivity regions for six neurons. The double boxes show the original at the upper part. The four examples shown in the upper two rows are considered separable in that the original and reconstruction are nearly identical. The two examples in the lower row represent cases in which some features are lost in the reconstruction; these were classified as doubtful cases. (B) Original and reconstructed spectro-temporal sensitivity regions for non-separable



cases. There is a gradually increasing difference between both representations. The loss of frequency-dependent latencies is particularly noteworthy: most of these units show double or multiple tuning. The vertical axis represents frequency on a logarithmic scale either ranging from 125 to 2000 Hz denoted by (1), or ranging from 250 to 4000 Hz indicated by (2). The horizontal axis represents time before the occurrence of the action potentials, running from right to left (compare Fig. 1), and is 128 ms except for unit 152-3 where the range is from 0 to 64 ms.

influenced by what we think is important for characterising the spectro-temporal receptive field. When at least three out of four agreed upon similarity or difference the classification was made accordingly, in other cases either equal votes or doubt expressed by the majority resulted in classification under the heading 'doubtful'.

In order to illustrate the criteria used we present in Fig. 2A results for six neurons in which four were judged to show no difference whatsoever between the original and the reconstructed spectro-temporal characterization and two neurons in which there was doubt. Fig. 2B shows six neurons which were considered as distinctly differing in the original and reconstructed properties. The upper part of each box shows the original, the lower part the reconstructed representation.

A few situations will serve to focus on the particular problems which arise when one has to make a choice between either spectro-temporal characterization or the use of independent spectral and temporal representations.

The upper left case in Fig. 2A (neuron 134-1) represents a neuron tuned around 675 Hz with a response time of 20–24 ms. The spectro-temporal characterization shows a symmetrical pattern along time as well as frequency axis; the reconstructed representation is identical to the original one. This neuron could have been characterized by its spectral and temporal properties without loss of information. Neuron 147-1 represents a multiple-tuned sensitivity range mainly centered around 750 Hz and 281 Hz, but with considerable high-frequency sensitivity as well, with equal latencies (about 50 ms) at both BFs. Although the reconstruction differs from the original we considered this to make no difference for a sufficient characterization of the neuron.

The case shown immediately below this one (137-5) represents multiple tuning in the high-frequency range (BF  $\approx$  1700 Hz) and in the mid frequency range (BFs equal to 750 and 525 Hz) with a slight latency difference at each BF being about 50 ms for the hf range and 54 ms for the mf range. The tuning properties are preserved in the reconstruction, the frequency-dependent latency of the neuronal response, however, is not preserved. It depends on the weight that one attributes to this property if one considers this a case where spectral and temporal properties still are independent. We classified this unit in the group of doubtful cases.

A somewhat clearer situation is provided by unit 166-5 shown in Fig. 2B. This unit again shows double tuning in the hf range and in addition mf sensitivity (BFs 1100 Hz and 525 Hz) but now with a considerable difference in response time at both BFs: 62 versus 78 ms. This important feature is completely lost in the integration and reconstruction procedure and we consider this as a case where separate study of tuning and timing properties could lead to erroneous interpretation of the neural properties. The most striking case of strong correlation between spectral and temporal properties is provided by unit 145-1. This particular unit shows a sensitivity over nearly the entire frequency range in which, however, several regions with larger sensitivity can be observed. The unit is sensitive at about 1 kHz with a latency of 38 ms and at 260 Hz with a latency of 62 ms. From the overall picture one observes that there is a smooth change of latency across frequency. In the reconstruction this is not preserved, but in addition the spectral width at the various BFs underwent some change as well as the temporal width at these BFs. We considered this case the most clear one in which one is not allowed to study independently tuning and timing properties.



TABLE I

COMPARISON OF THE ORIGINAL AND RECONSTRUCTED SPECTRO-TEMPORAL CHARACTERIZATIONS

Stimulus (ms)		Judgement			
Duration	Interval	Similar	Doubt	Different	Total
16	0	5	2	1	8
16	16	14	1	3	18
48	0	5	1	0	6
16	112	8	1	1	10
48	952	19	8	14	41
Total		51	13	19	83

An overall result for this classification, arranged according to the particular tone sequence needed for a stationary response, is shown in Table I.

It is striking that the necessity to use a 48 ms duration, 1 s silent interval sequence for a stationary response in fact is a selection criterion for the occurrence of a non-separable spectro-temporal characterization.

In order to relate this separability to some other characterizations of the neural unit we examined the distribution of the non-separable units over the various subdivisions of the torus semicircularis and the spike waveforms (Fig. 3) of the units. Between these

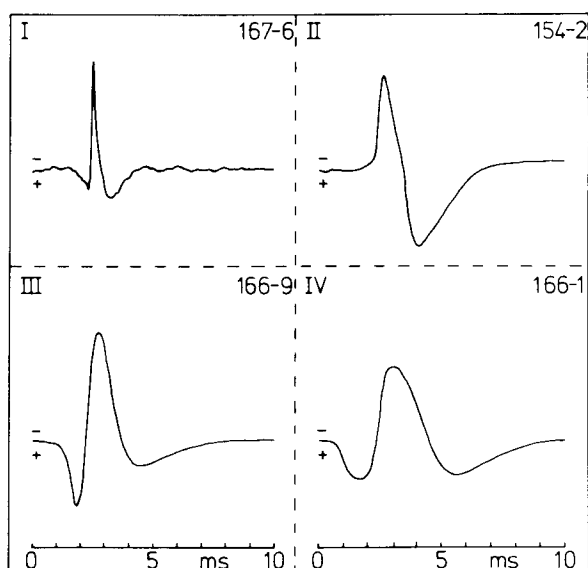


Fig. 3. Types of action-potential waveforms for neurons in the torus semicircularis. These types were obtained by subjecting a set of about 80 action-potential waveforms from different neurons to a pattern recognition procedure (data reduction by Karhunen-Loève expansion and clustering). Type I (upper left), consists of a fast axon-type spike, Type II a slower spike of about the same average amplitude (60–200  $\mu\text{V}$ ), Type III a large (>300  $\mu\text{V}$ ) spike, and Type IV represents a large (>300  $\mu\text{V}$ ) very slow action potential. Note that the recording temperature in the frog is about 15°C. (From [8]).

TABLE II

## DISTRIBUTION OF SEPARABLE AND NON-SEPARABLE UNITS OVER THE TORUS SEMI-CIRCULARIS AND RELATION TO SPIKE WAVEFORM

n.l., laminar nucleus; n.v., antero-ventral part of the principal nucleus; n.p., dorso-caudal part of principal nucleus; n.m., magnocellular nucleus; >t., outside torus semicircularis.

Spectro-temporal characteristics	Location in the torus semicircularis					Spike waveform			
	n.l.	n.v.	n.p.	n.m.	>t.	I	II	III	IV
Separable	14	16	13	1	1	15	1	29	3
Doubt	2	0	7	7	0	1	4	9	1
Non-separable	1	4	6	3	4	0	11	6	1

'non-response' properties of neurons and various other characterizations of the unit some correlations have recently been established [8].

It was found that non-separable units were located dominantly in the caudoventral parts of the torus or outside the torus, and that the absence of type I waveforms (probably related to incoming nerve fibers) and the relative abundance of type II waveforms (probably related to the multi-radiated cells in the central parts of the torus) deserves attention. The data are summarized in Table II.

In addition, all but one of the non-separable units had latencies in excess of 30 ms, while the overall latency distribution of units in the torus semicircularis showed for 95 units, 27 units with latencies shorter than 30 ms [8].

## DISCUSSION

The cross-correlation approach to study stimulus response relations for auditory neurons results in some average measure of the subset of stimuli to which the neuron responds. For primary auditory neurons this may be the signal value leading to an estimate of the impulse response of the auditory filter in case Gaussian wide-band noise is used as a stimulus. In the absence of phaselock — which is the case for the grass frog measured at a temperature of about 15°C for stimulus frequencies above 300 Hz — one may correlate with signal intensity or use a second-order cross-correlation approach [15]. By using a particular realization [16] this represents the average stimulus in the combined frequency-time domain. An adaptation of this method has been used for the set of narrow-band stimuli on which this study is based. Any correlation between frequency of the stimulus and time of occurrence before a spike can be related either to the peripheral frequency analyser or to convergence or interactions between neurons projecting onto the neurons in the torus semicircularis. For auditory neurons in the dorsal nucleus of bullfrogs Feng and Capranica [12] found latency differences of about 4 ms, probably attributable to the receptor properties. In the olivary complex Feng and Capranica [13] observed latencies ranging from 5–38 ms with a median of 14.5 ms at 10 dB above threshold.

The frequency-dependent latency criterium as used to judge, among others, the

similarity between original and reconstructed spectro-temporal representations generally required more than 4 ms latency difference at distinct BFs for classification in the non-separable group. It is tempting, therefore, to equate our criterion of non-separability to a complex convergence, or interaction, of neurons.

This assumption is supported by the high correlation between non-separability and type II spike waveforms. These spike waveforms are encountered exclusively in the ventral part of the torus semicircularis [8] where multiradiated cells are found [20,22], suggesting that converging input is likely. The fact that non-separability excludes Type I spike waveforms (fast axon-type spikes) as well as short latencies may in addition indicate that the convergence takes place in the torus semicircularis and not in lower centers of the frog's auditory system. This is supported by the absence of reports on double-tuned neurons in lower centers of the anuran auditory system [13].

The present results for auditory units in the torus semicircularis suggests that non-separability (23% of the neurons) is related to a high stage of information processing. An extrapolation to the auditory nervous system in mammals is not without danger, but separability and non-separability might be related to the subdivision of the ascending auditory information into the ventral and dorsal pathways which already show quite different response properties before they converge on the lateral lemniscus (e.g. [9,25]).

The practical implication would be that a separate measurement and study of tuning and timing properties of auditory neurons will be justified when investigating the ventral pathway. Studies on the dorsal pathway, including the dorsal cochlear nucleus, would benefit from a combined spectro-temporal approach, while for studies of stimulus-response relations in the inferior colliculus and higher centres the combined approach seems mandatory.

When one wants to avoid the presented cross-correlation type of approach in order to obtain a spectro-temporal representation, one may arrive at comparable results by measuring the tuning curve and PSTHs to tones having frequency and intensity values within this tuning curve [27].

The present report considers only single tone presentation, the situation might be more complex using two-tone stimuli or using wide-band noise. The justification for a combined spectro-temporal approach when using noise as a stimulus is amply discussed in Hermes et al. [15]. In these situations, however, the separation of  $I(f, t)$  into  $I_1(f)$  and  $I_2(t)$  so that  $\hat{I}(f, t) = I_1(f) \cdot I_2(t)$  might lead to  $I_1(f) = 0$  when determined by integration over the  $t$ -domain when, besides activation, post-activation suppression is also present. The same problems arise in the determination of  $I_2(t)$  in cases where lateral suppression occurs [15].

In conclusion, it seems well advisable to use a procedure, based on the presentation of a statistical stimulus ensemble of relatively long duration, which represents the spectral and temporal properties of neurons in an intricately coupled way, especially when studying parts of the higher central nervous system.

#### ACKNOWLEDGEMENTS

This research was supported by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.). Skillful assistance was provided by Wim van Deelen and Koos Braks in the various stages from animal preparation to data acquisition and analysis.

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