Beat-to-beat blood-pressure fluctuations and heart-rate variability in man: physiological relationships, analysis techniques and a simple model

de Boer, R.W.

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Chapter 4
The spectrum of a series of point events,
generated by the
Integral Pulse Frequency Modulation (IPFM) model

This chapter deals with the relation between the input-signal and the output-signal of the IPFM model (Chapter 2), a physiologically attractive model to describe the transformation of a continuous signal into a series of point events (spikes).

4.1 Abstract
The chapter deals with the relationship between the spectra of the input signal and the output signal of the Integral Pulse Frequency Modulation (IPFM) model. The IPFM model is a physiologically attractive device for the conversion of a continuous input signal into an output signal, consisting of a series of events (e.g., nerve spikes, heart beats).

Two different spectra are used in the analysis of a series of events: the interval spectrum and the spectrum of counts. The latter spectrum is analytically known for the event-series belonging to a sinusoidal input signal (Bayly, 1968). An approximation to the interval spectrum of this series is presented. Using data from a simulated IPFM model, it is shown that for an input signal consisting of the sum of two sinusoids, terms at sum and difference frequencies appear in the interval spectrum but not in the spectrum of counts. However, the spectrum of counts is contaminated by sidebands of the mean repetition frequency. It is concluded that in general the spectral properties of the input signal can not be recovered fully from the interval spectrum, nor from the spectrum of counts, the more so since physiological series of events will seldom be generated by an ideal IPFM model.

4.2 Introduction
Physiological series of point events, e.g. nerve spike-trains or series of heart beats, are often considered as the output signal caused by a less accessible, but physiologically relevant, input signal, e.g. the variability of heart rate is attributed to a varying amount of neural and humoral input to the cardiac pacemaker. Several au-
Thors have used the Integral Pulse Frequency Modulation (IPFM) model to recover the properties of the assumed input signal from the observed event series (for nerve spike trains: Bayly, 1968; Koenderink and Van Doorn, 1973; for heart-rate variability: Hyndman and Mohn, 1975; Rompelman et al., 1982; Chapter 2, or DeBoer et al., 1985a).

Essentially, the IPFM model (also called the Integrate to Threshold (ITT-)model) is a physiologically plausible device to transform a continuous input signal into an event series (fig. 1). The positive input signal, which consists of a DC-term (in fig. 1 taken as 1) and a modulating signal \( m(t) \), is integrated; whenever the integrated value \( y(t) \) exceeds a fixed threshold value \( I \), a spike (= an event) is generated and the integrator is reset. For a modulating signal \( m(t) = 0 \) the output signal \( x(t) \) is a regular spike-train, having constant intervals equal to \( I \).

In the application of the IPFM model to the analysis of physiological event series, one identifies the integrated signal \( y(t) \) with the membrane potential of an excitable cell; the potential rises until the threshold is reached, which causes an action potential (= an event) to occur. The modulating signal \( m(t) \) is considered as some external influence on the excitable cell, increasing or decreasing the rate of rise of the membrane potential.

\[ 1 + m(t) \]

\[ \int \]

\[ y(t) \]

\[ + \]

\[ \bar{I} \]

\[ \text{reset} \]

\[ x(t) \]

\[ t \]

Fig. 4-1 Diagram of the IPFM model: the input signal \( 1 + m(t) \) is integrated, and when the integrated value \( y(t) \) exceeds the threshold value \( \bar{I} \), a spike (event) is produced and the integrator is reset.

For \( m(t) = 0 \) (no modulation) the output consists of a regular spike train with constant interval \( \bar{I} \).
This chapter deals with the relationship between the spectrum of the continuous input signal and the spectrum of the event series (the output signal). It should be noted that two different spectral representations are used in the analysis of a series of point events: the interval spectrum and the spectrum of counts (Cox and Lewis, 1966; Chapter 3, or DeBoer et al., 1984). The former is the spectrum of the series of intervals, considered to be spaced at distances equal to the mean interval length $\bar{I}$. The latter, the spectrum of counts, is linked to the representation of a series of events as a train of mathematical deltafunctions.

The spectrum of counts is known analytically for the event series generated by a sinusoidally modulated input signal (Bayly, 1968); in this chapter we derive an analytical approximation to the interval spectrum of such a series. In addition we present the spectrum of counts and the interval spectrum for an input signal, consisting of two modulating sinusoids. It is shown that in the interval spectrum higher harmonics appear, as well as contributions at sum and difference frequencies.

The spectrum of counts is found to contain only sideband frequencies from the mean repetition frequency $1/\bar{I}$, apart from the fundamentals. We also pay attention to the spectrum of inverse intervals (heart-rate spectrum), as it has been suggested that this spectrum is superior to the interval spectrum (Mohn, 1976). In the conclusion we discuss to what extent the spectra of the event series resemble the spectrum of the input signal.

### 4.3 Methods

We obtained interval data by simulating an IPFM model on a digital computer. The interval spectrum and the spectrum of counts were calculated from these data as described in detail previously (Chapter 3, or DeBoer et al., 1984).

For the interval spectrum $A_I(f)$ a Digital Fourier Transform was used to calculate the periodogram of the normalized intervals $I_k = (I_k - \bar{I})/\bar{I}$, $\bar{I}$ being the mean interval length. A 10 per cent cosine taper was used. As the interval values are considered to be spaced at distances $\bar{I}$, the maximum frequency in the spectrum is $1/2\bar{I}$.

In the figures we present the amplitude-spectrum $A_I(f)$ rather than the usual power-spectrum $A_I^2(f)$ in order to stress the higher harmonics.

The spectrum of counts $A_C(f)$ is calculated as the spectrum of the dimensionless signal $p(t) = \sum_k \delta(t-t_k)$, with $t_k$ the time of occurrence of the events. The signal $p(t)$ has a mean value of zero, so no DC-component is present in the spectrum.
The spectrum of counts is, unlike the interval spectrum, not limited in frequency range, but usually only its low-frequency part is of interest. Therefore we show only this part of the spectrum in the figures. Spectral values were calculated for frequencies at intervals of 0.001 Hz.

4.4 The spectrum of counts and the interval spectrum of an IPFM process

4.4.1 Derivation of analytical expressions

An analytical expression for the spectrum of counts belonging to the input signal
\[ I + m \cos(2\pi f_m t + \phi) \]
was given by Bayly (1968): the spectrum consists of a DC-term, a term of relative amplitude \( m \) at frequency \( f_m \) and infinitely many sidebands, spaced at distances \( n f_m \) \((n = 0, \pm 1, \pm 2, \ldots)\) from multiples of the mean repetition frequency \( 1/\bar{I} \) (see Appendix 1). No higher harmonics of the fundamental frequency are present.

For a small modulation depth \( m \) the interval spectrum of this signal can be approximated as follows. The defining equation for the IPFM model is

\[ t_{k+1} - t_k = I, \]

with \( t_k \) the time of the \( k \)-th event, \( m(t) \) the modulating signal and \( \bar{I} \) the interval length if \( m(t) = 0 \) for all \( t \) (see fig.1). We put \( t_0 = 0 \). For a sinusoidal modulation one has

\[ \int_0^{t_k} (I + m \cos(2\pi f_m t + \phi)) \, dt = k\bar{I} \]

with \( f_m \) the modulation frequency \((f_m \ll 1/\bar{I})\). Performing the integration and writing \( t_k = k\bar{I} + \delta_k \) gives as a general relationship

\[ 2\pi f_m \cdot \delta_k \approx -m \cdot \left(1 - \left(1 - 2\pi f_m \delta_k \right)^2/2\right) \cdot \sin(2\pi f_m k\bar{I} + \phi) \cdot \cos(2\pi f_m k\bar{I} + \phi) \cdot \sin(\phi) \]

Hence, for a small modulation \((m \ll 1)\) the factor \( 2\pi f_m \delta_k \) is also small. Then, up to the second order:

\[ 2\pi f_m \cdot \delta_k \approx -m \cdot \left(1 - \left(1 - 2\pi f_m \delta_k \right)^2/2\right) \cdot \sin(2\pi f_m k\bar{I} + \phi) \cdot \cos(2\pi f_m k\bar{I} + \phi) \cdot \sin(\phi) \]

Hence

\[ \delta_k \approx -m \cdot \left(1 - \left(1 - 2\pi f_m \delta_k \right)^2/2\right) \cdot \sin(2\pi f_m k\bar{I} + \phi) \cdot \cos(2\pi f_m k\bar{I} + \phi) \cdot \sin(\phi) \]

Notice that in this approximation \( \delta_k \) may have large values if \( f_m \) is small, provided that \( 2\pi f_m \delta_k \ll 1 \). This extends the analysis of Chapter 3.4.2, where \( \delta_k \) was assumed to be small.
Putting $I_k = t_k - t_{k-1} = \bar{I} + \delta_{k} - \delta_{k-1}$ leads after some algebra to

$$I_k = 1 - m \frac{\sin(\pi f_m k \bar{I} + \phi_1) \cos(2\pi f_m k \bar{I} + \phi_1) - m \cos(\pi f_m k \bar{I}) \cos(4\pi f_m k \bar{I} + 2\phi_2)}{m \sin(\pi f_m k \bar{I})}$$

with $\phi_1 = \phi - \pi f_m \bar{I} m \sin(\phi)$ and $\phi_2 = \phi - \pi f_m \bar{I}$. Thus the first term of the interval spectrum has a relative amplitude $-m \sin(\pi f_m k \bar{I})/(\pi f_m k \bar{I})$ at frequency $f_m$. This is shown as a ratio of $\sin(\pi f_m k \bar{I})/(\pi f_m k \bar{I})$ between the amplitude of the first harmonic in the interval spectrum to the one in the spectrum of counts (or in the spectrum of the input signal). For $f_m \ll 1/\bar{I}$ (i.e. slow modulation) this ratio approaches 1. A second harmonic in the interval spectrum appears at frequency $2f_m$ with amplitude $m^2 \sin(\pi f_m k \bar{I}) \cos(\pi f_m k \bar{I})/(\pi f_m k \bar{I})$. For a slow modulation this can be approximated by $m^2$. The first-order term in $m$ in eqn.1 was given by Koenderink and VanDoorn (1973), who also presented an analytical expression for the event-times $t_k$.

A similar calculation shows that in the spectrum of inverse intervals, i.e. $I_k$ replaced by $1/\bar{I}_k$, the harmonic at frequency $f_m$ has an amplitude of $m \sin(\pi f_m k \bar{I})/(\pi f_m k \bar{I})$ and the second harmonic has an amplitude of $-m^2 (\sin(\pi f_m k \bar{I})/(\pi f_m k \bar{I}))(\cos(\pi f_m k \bar{I}) - \sin(\pi f_m k \bar{I}))/2(\pi f_m k \bar{I})$.

These expressions can be simplified for $f_m \ll 1/\bar{I}$: the amplitude of the first harmonic becomes $m$, of the second harmonic $-m^2/2$. The amplitude of the second harmonic is thus half its value in the interval spectrum. This result was suggested by Mohn (1976) on the basis of numerical simulations. He concluded that hence the spectrum of inverse intervals is a better approximation to the spectrum of counts than the interval spectrum. This point will be taken up later.

4.4.2 Experimental verification of the analytical results

To illustrate these results we present in figs.2a,b,c the interval spectrum (fig.2a), the spectrum of inverse intervals (fig.2b) and the spectrum of counts (fig.2c) for interval data produced by an IPFM model for an input signal $1 + m \sin(2\pi f_m t + \phi)$, with $m = 0.3$, $f_m = 0.16$ Hz and $\phi = 0$. The threshold was taken as 1.05 (s) and so the mean interval length was 1.05 s as well. 350 intervals were obtained by numerical simulation. It follows from eqn.(1) that a modulation depth of $m = 0.3$ results in intervals of which the length is up to approximately 30 per cent different from the main value.
Fig. 4-2  Spectra of a point event series generated by an IPFM model. The modulating input consists of a sinusoid with frequency 0.16 Hz. Figs. 2a and 2b are the interval spectrum and the spectrum of inverse intervals, respectively. These are the spectra of the (inverse) interval values, considered to be spaced equidistantly at distances equal to the main interval length, 1.05 s. Hence the maximum frequency in these spectra is $1/(2 \times 1.05) = 0.476$ Hz. Fig. 2c is the spectrum of counts. In the computation of this spectrum, the events are considered as mathematical delta functions. Note the presence of higher harmonics in figs. 2a, b and of sidebands of the mean repetition frequency ($1/1.05 = 0.952$ Hz) in fig. 2c.

The presence of higher harmonics in the spectra is evident in figs. 2a, b. The second harmonic in the interval spectrum is approximately two times larger than in the spectrum of inverse intervals, which agrees with the analytical treatment given above. The two peaks in the spectrum of counts (fig. 2c) at frequencies 0.312 Hz and 0.472 Hz are sidebands, located at four and three times 0.16 Hz respectively from the mean repetition frequency ($1/1.05 = 0.952$ Hz). The amplitudes of the
peaks in figs.2a-c are explained quantitatively in Appendix A1. The main peaks in the spectra are accompanied by a number of smaller ones at distances \( \frac{1}{(N_i)} = 0.0027 \) Hz, due to the windowing effect of the limited data length. The tapering as used in the Digital Fourier Transform (figs.2a,b) reduces this effect (cf. fig.2c).

4.4.3 The sum of two sinusoids

The case of a modulating signal consisting of the sum of two sinusoids is more complicated. As an example we present spectra for data from the IPFM model for an input signal \( 1 + m_1 \sin(2\pi f_m_1 t + \phi_1) + m_2 \sin(2\pi f_m_2 t + \phi_2) \), with \( m_1 = m_2 = 0.3, f_m_1 = 0.12 \) Hz, \( f_m_2 = 0.16 \) Hz and \( \phi_1 = \phi_2 = 0 \). Again, the threshold is 1.05 s. The interval spectrum (fig.3a) and the spectrum of inverse intervals (fig.3b) contain terms at sum- and difference-frequencies of the two modulating frequencies. Note, for example, adjacent to the peak at 0.40 Hz \( f = 2 \times 0.12 + 0.16 \), the small peak at

![Graph](image-url)
0.392 Hz in fig.3a which is the contribution at the double-sum frequency \((2 \times (0.12 + 0.16) = 0.56 \text{ Hz})\) folded back due to aliasing (the apparent Nyquist frequency is \(1/(2 \times 1.05) = 0.476 \text{ Hz}\)). The terms at sum frequencies are larger in fig.3a than in fig.3b; on the other hand, the term at the difference frequency \((0.16-0.12 = 0.04 \text{ Hz})\) is much larger in fig.3b than in fig.3a.

Table 1 shows how all peaks in figs.3a,b can be attributed to sum and difference frequencies. It is seen that some peaks coincide due to our choice of modulating frequencies; e.g. the peak at 0.20 Hz is made up of contributions at \((2 \times 0.16-0.12)\) Hz and at \((3 \times 0.12-0.16)\) Hz.

<table>
<thead>
<tr>
<th>TABLE 1</th>
<th>TABLE 2</th>
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<tr>
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<td>peak (Hz)</td>
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<td>(2f_1+3f_2)</td>
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<td>0.272</td>
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<tr>
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<tr>
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<td>0.392</td>
</tr>
<tr>
<td>(f_1+f_2)</td>
<td>(f_R - (2f_1+2f_2))</td>
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<td>0.432</td>
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<tr>
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<td>(f_R - (3f_1+2f_2))</td>
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<td>(f_1+2f_2)</td>
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<td>0.472+ (0.48)</td>
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**Table 1** Attribution of the main peaks in figs.3a and 3b to sums and differences of the modulating frequencies \(f_1 = 0.12 \text{ Hz}\) and \(f_2 = 0.16 \text{ Hz}\). The marked values (*) are due to aliasing; the Nyquist frequency is \(1/\bar{T} = 0.476 \text{ Hz}\).

**Table 2** Attribution of the main peaks in fig.3c to sideband frequencies of the mean repetition frequency \(f_R = 1/\bar{T} = 0.952 \text{ Hz}\).
Terms at sum and difference frequencies of the fundamentals (0.12 Hz and 0.16 Hz) are absent in the spectrum of counts (fig.3c and table 2), although their presence has been reported earlier (Koenderink and VanDoorn, 1973) due to confusion of these terms with some of the many sidebands of the repetition frequency (cf. Coenen et al., 1977). (This point is discussed further in Appendix A2). However, sum and difference frequencies do appear in the sidebands; e.g., the contribution at 0.272 Hz is a sideband at distance 0.68 Hz ( = 3x0.12+2x0.16) from the mean repetition frequency 0.952 Hz.

4.5 Conclusion

The interval spectrum belonging to a sinusoidally modulated input signal contains harmonics at sum and difference frequencies of the constituents of the input signal (figs.2a,3a). In the spectrum of inverse intervals the harmonics at sum frequencies are smaller (figs.2b,3b), but, as the harmonics at the difference frequency are much larger, we do not think that much is gained by the use of inverse intervals instead of intervals in computing the spectrum. The analysis given shows that the amplitude of the interval spectrum is \( \sin(\pi f) / (\pi f) \) times the amplitude of the spectrum of the input signal. Consequently, contributions at higher modulation frequencies will appear somewhat reduced in the interval spectrum. This corresponds to the results we found for heart-rate variability spectra (Chapter 3, or DeBoer et al., 1984). The peaks due to aliasing in fig.3a contradict the assumption of Musha et al. (1983) that one does not need to take aliasing into account when using the interval spectrum (see also fig.A1a in Chapter 3).

The spectrum of counts seems the most logical choice for spectral analysis of an events series produced by an IPFM model, as it reproduces the spectrum of the input signal without introducing new harmonics. However, the contributions of the sidebands of the mean repetition frequency may obscure the spectrum in demand (figs.2c,3c), the more so for larger modulation depths and higher modulation frequencies. The sidebands would have appeared less important if power-spectra were presented in our figures instead of amplitude-spectra.

The spectrum of an input signal that consists only of a few sinusoids can theoretically be retrieved from the spectrum of counts (e.g., the input signal belonging to the spectrum of fig.3c can easily be found). The continuous spectrum of a general input signal is not so easy to extract from the spectrum of counts, nor from the
interval spectrum. However, too much precision in this respect will in most cases hardly be meaningful, as physiological event series will seldom be generated by a perfect IPFM system, and so additional harmonics of the input signal will appear in the spectrum of counts as well as in the interval spectrum.
4. Appendix 1: The amplitudes of the spectral peaks in figs.2a-c
In the case of figs.2a-c, the event series \( p(t) \) originated from the input signal
\[ l + m \cdot \cos(2\pi f_m t) \] with \( m = 0.3 \) and \( f_m = 0.16 \) Hz. This event series can be written as a sum of sinusoids (Bayly, 1968):
\[ p(t) = \sum_k \delta(t-t_k) = 1 + m \cdot \cos(2\pi f_m t) + \sum_{n=1}^{\infty} \frac{a_n \cdot \cos(2\pi (k f_R + n f_m) t)}{k} \] (A.1)

with \( a_n = (1 + n f_m / k) \cdot J_n(k m / f_m) \), \( J_n \) a Bessel-function of order \( n \) and \( f_R = 1/1.05 = 0.952 \) Hz. The spectrum of counts is the spectrum of the signal \( p(t) \). Eqn. A.1 shows contributions to exist at the modulation frequency \( f_m \) and at frequencies \( k f_R + n f_m \) for \( k > 1 \) (sidebands from the main repetition frequency).

To illustrate this equation, we show in fig.A1 once again the spectrum of counts of Fig.2c, but now for a larger frequency range up to 1.25 Hz; spectral values are now calculated each 0.0025 Hz, which leads to some aliasing in the minor peaks around the major peaks (e.g., compare the minor peaks around 0.16 Hz in Fig.2c and in the present figure). The large contribution at \( f_R = 1/1.05 \) Hz and the many sidebands, predicted by eqn. A.1, are seen.

Eqn. A.1 is useful to assess the relative amplitudes of the peaks in fig.A1. In the following we give an quantitative analysis of these amplitudes. An estimate of the power spectrum \( G(f) \) of a signal \( x(t) \), calculated over the interval 0 till \( t_{max} \) is (Bendat and Piersol, 1971, eqn.9.134):

![Fig.4-Ala Spectrum of counts for a sinusoidally modulated input signal (f_m = 0.16 Hz) over the range 0-1.25 Hz (cf. Fig.2c). Note the contributions at 0.16 Hz, at 0.952 Hz and at 0.952±0.16 Hz, 0.952±0.32 Hz, etc. (0.952 = 1/1.05 is the mean repetition frequency). The figure is conform eqn.A.1.](image-url)
\[ G(f) = \frac{2}{t_{\text{max}}} \left| \int_{0}^{t_{\text{max}}} x(t) \exp(-2\pi ift) \, dt \right|^2. \]

For a sinusoidal signal \( x(t) = A \cos(2\pi f_m t) \), \( G(f) \) can be calculated for \( f = f_m \) as:

\[ G(f_m) = \frac{A^2 t_{\text{max}}}{2} \left( \frac{1}{1 + O(1/t_{\text{max}})} \right) \]

Hence, for \( t_{\text{max}} \rightarrow \infty \), \( G(f) \) consists mainly of a peak at frequency \( f_m \) with amplitude \( A^2 t_{\text{max}} / 2 \) and width inversely proportional to \( t_{\text{max}} \).

We calculated in fig.2c (and in fig.A1) the spectra for a signal of length \( t_{\text{max}} = 350 \) and therefore the amplitude spectrum should have a peak at \( f = f_m = 0.16 \) Hz of height \( (A^2 t_{\text{max}} / 2)^{1/2} = 4.07 \), which is in agreement with fig.2c. The amplitudes of the sideband peaks can be calculated using eqn.A.1; for \( k = 1 \) and \( n = -3 \) (\( f = 0.472 \) Hz) or \( n = -4 \) (\( f = 0.312 \) Hz) the result is 1.30 and 0.20, respectively; these values are also in agreement with fig.2c.

According to section 4.4.1 the approximate amplitude of the peak in the interval spectrum at 0.16 Hz should be \( \sin(\pi f_m t_m) / (\pi f_m t_m) \) times the one in the spectrum of counts, leading to the value 3.88; the harmonic at 0.32 Hz should have amplitude 1.01 (cf. fig.2a). For the spectrum of inverse intervals, these values are 3.88 (0.16 Hz) and 0.40 (0.32 Hz) (cf. fig.2b). It is seen that the theoretical values correspond well with the computed ones.

When comparing theoretical and computed spectra, often no computed value is available exactly at the peak of the spectral components. For example, in fig.2c we computed the spectrum of counts for frequency values 0.001 Hz apart; however, the largest sideband contribution in this figure is at 1/1.05-0.48 Hz = 0.47238... Hz and no value is computed at exactly this frequency. If the peak is narrow, our computed values at 0.472 Hz and 0.473 Hz will both underestimate the amplitude of the peak.

In a similar way, the effective frequency resolution for a 1024-point Digital Fourier Transform as used for the interval spectrum is 1/(1.05x1024) = 0.000930... Hz. Hence our choice of modulating frequencies 0.12 Hz and 0.16 Hz in Figs.2,3: the 129-th spectral component is at 129x0.000930 = 0.11998 Hz, the 172-th component is at 172x0.000930 = 0.15997 Hz. These two components will therefore fairly
well represent the true amplitude of the peaks at 0.12 Hz and 0.16 Hz, respectively. We also limited the length of the event-series to 350 data points, because a longer series produces narrower peaks and hence the above-described problems become more important.

As an example of the use of the French-Holden algorithm (Chapter 3.A2), we show in fig.4.A1b the spectrum of counts calculated by this algorithm for the sum of two sinusoids (cf. fig.3c). Not surprisingly, figs.3c and A1b are very alike.

4.A2 Appendix A2: Sum frequencies in the spectrum of counts?
Koenderink et al. (1973) stated that sum and difference frequencies of the modulating sinusoids exist in the spectrum of counts. Their fig.8 was to prove this. We reproduce this figure in our format in Fig.A2a. It is the spectrum of counts for IPFM data, derived from an input signal, that consists of the sum of two sinusoids with frequencies of 0.07 Hz and 0.30 Hz. The repetition frequency is 0.37 Hz (mean interval 2.7 s). At first sight, peaks at sum and difference frequencies seem to be present in this spectrum: for example, the peak at 0.14 Hz can be explained as 2x0.07 Hz, and the one at 0.23 Hz as 0.30-0.07 Hz.

However, if the spectrum is computed for modulating frequencies 0.07 Hz and 0.28 Hz (fig.A2b) instead of 0.07 Hz and 0.30 Hz (Fig.A2a), the above explanation would predict that the 0.14 Hz-peak remains and that the 0.23 Hz-peak shifts to 0.21 Hz (≈ 0.28 Hz-0.07 Hz). In reality, Fig.A2b shows no peak at 0.14 Hz, nor a peak at 0.21 Hz, but a peak at 0.23 Hz is still present. This -- and similar results
from further examples -- can only be explained if another origin of the peaks is assumed. The 0.14 Hz contribution in Fig.A2a originates as a superposition of 2x(0.37-0.30) Hz and 3x(0.37-0.30)-0.07 Hz, and hence splits up in Fig.A2b in contributions at 2x(0.37-0.28) = 0.18 Hz and at 3x(0.37-0.28)-0.07 = 0.20 Hz. Peaks are indeed seen at these positions in Fig.A2b. The position of the 0.23 Hz peak does not change between Figs.A2a and A2b; this is to be expected if the 0.23 Hz is seen as due to 0.37-2x0.07 Hz, which is not influenced by the change of the second modulating frequency.

We are not able to explain all peaks in the spectra of Figs.A2a,b in detail. An exhaustive analysis is difficult, due to the multitude of coinciding peaks in the spectra. However, our analysis shows that it is quite unlikely that sum and difference frequencies of the modulating frequencies are present in the spectrum of counts.

![Fig.4-A2a](image1)

**Fig.4-A2a** Spectrum of counts for an input signal, consisting of the sum of two sinusoids of frequencies 0.07 Hz and 0.30 Hz (arrows; as in Koenderink et al., 1973, Fig.8). Contributions at the sum- and difference-frequencies seem to be present (e.g., at • 0.14 Hz = 2x0.07 Hz, or at * 0.23 Hz = 0.30-0.07 Hz). Horizontal: frequency (Hz), vertical: power (arbitrary units).

![Fig.4-A2b](image2)

**Fig.4-A2b** As Fig.A2a, but now for frequencies of 0.07 Hz and 0.28 Hz. No peaks are seen at 0.14 Hz or 0.21( = 0.28-0.07) Hz. This contradicts the assumption that contributions at sum and difference frequencies are present in fig.A2a. For further discussion see text.