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A Comparison of Results from Parameter Estimations of Impulse Responses of the Transient Visual System*

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Abstract. Parameter estimations of a fourth-order linear model are applied to data from subthreshold measurements of impulse responses of the transient visual system. These impulse responses were obtained experimentally by several subjects, at two different background luminance levels and for different field sizes. The parameter estimations show consistent results over different subjects. For both different background levels and field sizes there are consequent changes in the estimated parameters. On the basis of these changes a proposal is made for a spatiotemporal model of the transient visual system.

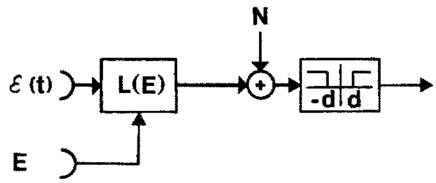

Fig. 1. The model for the transient channel: a linear filter L, an additive noise source N, and a detection mechanism with threshold d

1 Introduction

It is generally agreed that the human visual system processes stimuli in different parallel subsystems, called channels. In the temporal domain two channels are usually assumed: the *sustained* and the *transient* channel. The simplest model for a single channel is given in Fig. 1, and consists of a linear filter L followed by an additive noise source N and a detection mechanism with threshold d. The linear filter characteristics depend on the (mean) background, the spatial dimension of the stimulus and surprisingly little on the subject, as will be shown.

Many attempts have been made to model the temporal behaviour of the visual system at threshold level from experimental data of the frequency domain; Kelly (1971b); Roufs (1972b); Georgeson (1987); Ohtani and Ejima (1988), to name just a few. There are three major problems in this approach. First, to model the system from De Lange data (modulation or amplitude sensitivity as a function of the frequency of sinusoidally modulated light) leaves out the problem of in parallel operating channels. Second, stochastic effects contribute to De Lange curves (cf. Roufs 1974b) and it is not known whether these effects have equal contributions to the sensitivities at different frequencies. Third, the phase characteristic of the system is unknown. These problems for modelling from De Lange data are usually solved on an ad hoc basis, but in most cases cause a conflict in the prediction of the behaviour of the system and the experimental results of pulse-like stimuli (especially the Broca-Sulzer phenomenon which can be found at threshold level under certain experimental conditions, cf. Roufs 1974a; Georgeson 1987; Ohtani and Ejima 1988). Another approach was therefore chosen by Roufs and Blommaert (1981) and Blommaert and Roufs (1987), who found that it is possible to measure separately the impulse responses associated with the transient and sustained channel. In this study the experimental data from Roufs and Blommaert (1981) and Blommaert and Roufs (1987) on impulse responses of the *transient channel* is used to model this system. It is shown that the estimated model agrees with experimental data from the spectral domain (Sect. 6).

By means of a perturbation technique it is possible to measure the impulse response of the transient and sustained channel of the human visual system (Roufs and Blommaert 1981). Such an experiment has been

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carried out by different subjects at different background levels (Roufs and Blommaert 1981; Blommaert and Roufs 1987) and for different field sizes. The results of these measurements show a triphasic impulse response for large field sizes (i.e. diameters larger than approximately 0.3 deg). This response is associated with the *transient* visual system (Roufs 1974a; Roufs and Blommaert 1981).

In this paper it is shown that these triphasic impulse responses can be adequately modelled as a fourth-order linear filter. In the Laplace domain this linear filter is described as a transfer function with two complex pole pairs, one zero and an amplification factor (den Brinker and Roufs 1989). In this article, the parameters and 90% confidence regions obtained by the estimation process described by den Brinker and Roufs (1989) are compared over the different experimental conditions under which the impulse response measurements were performed.

This comparison of estimated parameters (poles and zeros of the transfer function) of the linear filter might give information about the behaviour of the system with varying experimental conditions. In this way this analysis can give insight into the fundamental properties of the processing of visual stimuli, and might provide a link with the experimental results obtained by electrophysiology. As far as we know, this kind of research of systematic changes in parameters of a linear filter as a function of experimental conditions has not been performed before, except in more general terms, where characteristic quantities (cut-off frequency, sensitivity) have been experimentally determined as a function of background (Kelly 1961; Roufs 1972a) and spatial dimension (Roufs and Bouma 1980).

The estimated parameters show that there are relatively small intersubject variations of their values if the same background and the same spatial configuration of the stimulus are used. Over different background levels there is a consistent change in the measured impulse response. The measured impulse responses seem to be isomorphic (Roufs 1974a; Roufs and Blommaert 1981). The change of the measured impulse response is reflected in a change of the estimated parameters of the fourth-order linear filter. From the fourth-order linear filter estimates it is found that for the largest part there is indeed a change in time scale. As a second minor effect a change in the lowpass behaviour occurs. Together this means that the impulse responses at different levels are indeed approximately isomorphic, though not precisely as Roufs (1974a) assumed.

Variation of the field size (for one subject and one background level) results in a change of the measured impulse response. These changes are reflected in the parameters of the estimated filter. It will be shown that only part of the estimated parameters vary with a change in spatial configuration. This implies that it is possible to isolate the lateral and the afferent information spread contained in these impulse responses. On the basis of this finding a simple *spatiotemporal* model for the transient visual system is proposed.

In the last part of the article we will show that the impulse response data and the analysis of the behaviour of the parameters of the linear filter are in agreement with other experimental findings, most notably the measurements of the sensitivity versus the frequency of a sinusoid, the so-called De Lange curves.

The modelling performed here is a black-box approach. The importance of such a model for psychophysical behaviour is given by its generalizing and predictive properties [see also Sect. 6, Blommaert and Roufs (1987), and den Brinker and Roufs (1989)]. The actual neuronal implementation is not our first concern; we did not to incorporate neurophysiological concepts into the model (i.e. a grey-box approach) since it is not sure which physiological data would be appropriate to constitute the material for a psychophysical model. This issue remains a problem, since what is known from physiology are mostly single cell responses, while psychophysical responses involve the activity of masses of cells.

Still, the model that is finally found shows changes in estimated parameters with experimental condition (background level and field size). For the variation of the estimated parameters with field size it is argued (Sect. 7) that this implies a separate spatiotemporal operator as a subsystem within the transient channel *at least* functionally. However, the fact that the parameter changes occur so consistently is interpreted as a sign that there may be more than just a functional relation and that the subprocess that is found from these functional analysis may have an actual neuronal counterpart. In that case the modelled system (and its basic functions: damped sinusoids) must be seen as a rough approximation to underlying neuronal processes; in this view a complex conjugated pole pair (i.e. a damped sinusoid) may be seen as an approximation to biphasic impulse responses as are frequently measured in retinal cells (cf. Enroth-Cugell and Shapley 1973; Naka 1982; Kawasaki et al. 1984; Daly and Normann 1985). Since our aim is to obtain an adequate and simple predictive psychophysical model and since the relation with physiological data is far from obvious, we will refrain from any detailed comments on this subject. The best we can *hope* for (see Sect. 7) is that at some later point the model presented here proves to be compatible with neurophysiological points of view.

2 Measurement Data, the Description of the Fourth-Order Linear Filter and Evaluation of the Fit

Available Experimentally Obtained Impulse Responses

The experimentally obtained impulse responses that are available and considered here are:

- impulse responses of seven subjects at a 1200 Td level for a 1 deg field,
- impulse responses of three subjects at a 100 Td level for a 1 deg field,
- impulse responses of two subjects at a 1200 Td level for different field diameters.

How these impulse responses are derived experimentally is not an issue in this paper (see Roufs and Blommaert 1981). The measured impulse responses are estimated as a fourth-order linear filter with a transfer function described by two complex pole pairs and one zero. The parameter estimation technique is described elsewhere (den Brinker and Roufs 1989), and extended by estimates of the 90% confidence regions of the parameters. The estimates of the confidence region are only appropriate if the objective function in the optimization problem is (approximately) quadratic within these regions. In all cases a check was made on this assumption. In this paper we will concentrate on the results of these parameter estimations. In cases where estimated parameters are compared over different experimental conditions, and parameter shifts are supposed to result from the changed experimental conditions, support for this reasoning will be sought from the estimates of the confidence regions, insofar as these could be estimated.

The Transfer Function of the Linear Filter

As a linear model for the transient system a fourth-order filter is used, with transfer function $H(s)$ in the Laplace domain s. The transfer is given in threshold units d (see Fig. 1). The characteristics of the filter are described by its parameters (p_1, p_2, z, A, NF) according to

$$H(s) = NF \frac{A(s-z)}{(s-p_1)(s-p_1^*)(s-p_2)(s-p_2^*)}, \tag{1}$$

where

NF = norm factor,

A = an amplification factor,

z = a zero of the transfer function,

p_1, p_2 = complex poles of the transfer function,

$*$ = the conjugate of a complex number.

The impulse response $h(t)$ can be calculated from $H(s)$ as

$$h(t) = NF \cdot A \sum_{i=1}^{2} \{R_i \exp\{p_i t\} + R_i^* \exp\{p_i^* t\}\}, \tag{2}$$

where R_i are the (complex valued) residues given by

$$R_1 = \frac{p_1 - z}{(p_1 - p_1^*)(p_1 - p_2)(p_1 - p_2^*)}, \tag{3}$$

$$R_2 = \frac{p_2 - z}{(p_2 - p_1)(p_2 - p_1^*)(p_2 - p_2^*)}. \tag{4}$$

Some examples of measured and estimated normalized impulse responses are shown in Fig. 4 and will be discussed later. All estimated impulse responses mentioned in this article and not shown in Fig. 4 can be found in den Brinker and Roufs (1989). As a result of the measurement technique the measured impulse response is basically scaled to an extreme equal to one, the absolute value being obtained separately. The amplification factor A is such that the fitted curve $H(s)/NF$ has an extremum exactly equal to one.

The filter $H(s)$ given by (1) is the transform of an impulse response that consists of a sum of damped sinusoids (2). If this description is to supply insight into the processing within the transient channel, it presupposes that different subsystems within this channel can *approximately* be described by impulse responses that are damped sinusoids. Conceptually, this is not unlikely: many physiological experiments and models describe feedback mechanisms (e.g., adaptive models; Shapley and Enroth-Cugell 1984). Such mechanisms often show these oscillatory responses as a direct consequence of the feedback loop. In actual measurements of single neurons mostly biphasic impulse responses are found (e.g., Naka 1982; Daly and Normann 1985). If the real part of the poles is not too small with respect to its imaginary part, the impulse response associated with a complex conjugated pole pair can be considered as an approximation to these responses. From this point of view the filter (1) may not only provide descriptive formula of the impulse response, but may also be able to reveal the underlying properties of the temporal processing.

Estimated and Measured Noise

Given the experimental uncertainty the fits agree reasonably well with the measurements. This is shown numerically in Table 1. Here we have compared the mean measured and the estimated noise given by the standard deviations. The mean measured standard deviation s_m is taken as

$$s_m^2 = \frac{1}{M} \sum_{i=1}^{M} s^2(t_i), \tag{5}$$

where

M = the number of samples,

t_i = the sampling moments of the impulse response, $1 \leqq i \leqq M$,

$s(t_i)$ = the measured standard deviation of the mean at t_i.

For the estimated standard deviation s_e we find (Bard 1974; Wolberg 1967)

$$s_e^2 = \frac{\Psi}{M-N}, \tag{6}$$

where

Ψ = sum of squared residuals at the final estimate,

M = number of measured samples,

N = number of degrees of freedom in the estimation process, $N=5$ (den Brinker and Roufs 1989).

Table 1 shows that the estimated standard deviation is in most cases greater than the measured standard deviation. Some of the fits, notably FB and JW, are not adequately represented by the fourth-order filter. Probably a higher order filter would be better. However, averaged over different subjects the estimated standard deviation s_e is only about 8% larger than the measured standard deviation s_m. Therefore, we argue that in most cases a fourth-order filter is a sufficiently elaborate model to represent the measured impulse responses. Furthermore, we will show that, even in cases of poorer fits, the estimated fourth-order linear filter shows a consistent parameter set.

Table 1. Measured standard deviation s_m and the calculated standard deviation of the noise. The estimated noise for a model according to (1) is denoted by s_e; for the same model but now with $z = 0$ (a bandpass filter) the noise is denoted as s_b

	Background (Td)	Field size (deg)	s_m	s_e	s_b
JR74	1200	1	0.120	0.144	0.157
JAJR	1200	1	0.086	0.099	0.111
FB	1200	1	0.074	0.127	0.0
JP	1200	1	0.112	0.131	0.139
LT	1200	1	0.139	0.115	0.131
HD	1200	1	0.118	0.143	0.144
IH	1200	1	0.106	0.154	0.156
LT	100	1	0.109	0.096	0.180
HR	100	1	0.113	0.116	0.217
JW	100	1	0.170	0.247	0.252
HD	1200	0.28	0.168	0.145	0.219
HD	1200	1.00	0.118	0.143	0.144
HD	1200	5.50	0.124	0.111	0.179
IH	1200	0.28	0.153	0.087	0.106
IH	1200	0.50	0.152	0.126	0.128
IH	1200	1.00	0.106	0.154	0.156
IH	1200	5.50	0.093	0.078	0.148

Apart from the above-mentioned estimations we also fitted the same fourth-order filter (1) with a bandpass restriction, i.e. $z=0$. In the fits of the data to a bandpass filter only the complex pole pairs acted as degrees of freedom in the estimation process. The results of the bandpass estimates show that the fits to this model are not as good as those with z as a free parameter. Not only is the estimated standard deviation σ_b in all cases greater than σ_e (see Table 1), but also that these fits always overestimated the first (negative) phase. The reason for estimating a bandpass filter for the transient system is that in contrast to usual assumptions about the transient system (Roufs 1974a), our model [given by (1)] has spurious sustained activity; its response to a step function shows a large response at the onset, but also a small steady response for long durations after onset.

3 Intersubject Variations of Estimated Parameters

First, the intersubject variations of the estimation results for a 1 deg field without surround will be considered. The estimated parameters for seven subjects at a 1200 Td background level and three subjects at 100 Td are shown in Table 2. The first columns contain the estimated parameters p_1, p_2, and z. The complex values p_1 and p_2 are split up into two real valued parameters:

$$p_i = \alpha_i + j\beta_i, \quad i = 1, 2, \tag{7}$$

where $j = \sqrt{-1}$ and $\alpha_i, \beta_i \in \Re$ $(i=1,2)$. α_i is the i-th damping parameter and β_i the i-th angular frequency parameter. The pole p_1 is the pole with the largest norm. The last two columns contain the amplification A and the norm factor NF. The amplification A was not a free parameter in the estimation process but was calculated to obtain an extremum of the impulse response equal to one (den Brinker and Roufs 1989). The norm factor NF gives the experimentally measured sensitivity of the system to an impulse, and is expressed in units $\mathrm{Td}^{-1}\,\mathrm{s}^{-1}$. Together the parameters in Table 2 describe the system in threshold units d. The impulse response $h(t)$ can now be given in these damping and frequency parameters by

$$h(t) = NF \cdot A \sum_{i=1}^{2} B_i \exp\{\alpha_i t\} \cos(\beta_i t + \phi_i), \tag{8}$$

where $R_i = 0.5 B_i \exp\{-j\phi_i\}$.

Table 2. Estimated parameters of the fourth-order linear filter for seven subjects at a 1200 Td level and three subjects at a 100 Td level (upper and lower part of the table respectively). In all cases the stimulus diameter is 1 deg

	α_1 (s^{-1})	β_1 (rad/s)	α_2 (s^{-1})	β_2 (rad/s)	z (s^{-1})	A ($10^4\,s^{-2}$)	NF ($Td^{-1}s^{-1}$)
JR74	−25.0	83.6	−15.4	42.1	6.87	−0.946	0.68
JAJR	−27.6	93.8	−15.4	46.5	13.6	−1.07	0.90
FB	−20.5	101.0	−12.9	54.1	19.2	−0.874	1.2
JP	−22.5	94.1	−18.8	44.8	13.2	−1.04	1.09
LT	−20.4	94.3	−20.2	54.0	20.2	−0.935	0.59
HD	−23.3	99.8	−19.3	51.8	11.8	−1.13	0.44
IH	−19.8	103.0	−22.0	50.2	53.8	−0.833	1.01
LT	−16.6	56.1	−20.8	26.6	20.1	−2.11	3.86
HR	−13.0	58.5	−14.1	28.0	32.9	−3.47	7.46
JW	−10.1	58.1	−11.8	28.8	17.8	−3.38	4.59

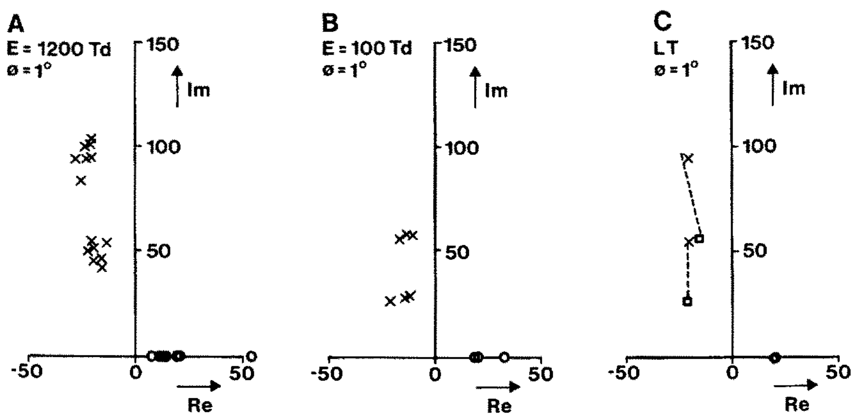


Fig. 2A–C. Pole-zero plots in the complex plane. Horizontal and vertical axes are the real and imaginary axes, respectively. The units are in s^{-1}. The lower part of the s-plane is not shown in this plot. **A** Estimated parameters of all impulse responses at 1200 Td. The crosses and circles are the poles and zeros, respectively. **B** Estimated parameters of all impulse responses at 100 Td. The crosses and circles are the poles and zeros, respectively. **C** Estimated parameters of subject LT at 100 and 1200 Td. The crosses and circle are the poles and zero, respectively, at 1200 Td. The squares and diamond are the poles and zero, respectively, at 100 Td. The dotted lines give the direction of the movement of the poles p_1 and p_2 with variation in background

From Table 2 we see that the variation of the estimates over the different subjects is relatively small, given a specific background level. This is also shown in Fig. 2A and B. In Fig. 2A the estimated poles and zeros of seven subjects at the 1200 Td level are shown, in Fig. 2B the estimated poles for three subjects at 100 Td. From these plots it can be seen that there are only minor variations between subjects if identical spatial configuration and background level are used. All parameters p_1, p_2, and z cluster, at both 1200 (Fig. 2A) and 100 Td background (Fig. 2B). At 1200 Td there is one zero (for subject IH, see Table 2) which has an exceptional location with respect to the cluster formed by the other zeros. But then, this zero has a large variance as can be seen from the 90% confidence intervals shown in Fig. 5B (this figure will be discussed later).

Comparing Fig. 2A and B we see that a change in background level shows a much larger change in the estimated parameters than the intersubject variation at one level.

4 Changes in Estimated Parameters with Background

In Sect. 3 it was shown that at one background level for a certain spatial configuration (1 deg field) the estimated parameters for different subjects have only minor variations. We now try to establish invariances over the two background conditions that were used in the experiments.

First, we will argue that the zero z is nearly independent of the background. From Table 2 it can be seen that this parameter for different subjects lies roughly between 10 and 25 s^{-1} for both levels (except for IH). But, more important, the results for subject LT, from whom impulse responses at both levels are available, show an estimated zero that is nearly identical at both levels. A similar argument holds for the damping parameter α_2. This is also illustrated in Fig. 2C where the estimated poles and zeros of subject LT at both levels are simultaneously plotted.

As a second source of information on invariances over both background levels, we look at the *relative location* of these parameters in the s-plane, i.e. we ignore the absolute values of the parameters, but consider the *ratio* of the different parameters.

This is tabulated in Table 3. The two last columns give the ratio $-\alpha_1/\beta_1$ and $-\alpha_2/\beta_2$. This ratio is a measure of the direction of these poles in the s-plane. In columns three and four the ratios α_1/α_2 and β_1/β_2 can be found, which relate the location of pole p_1 to pole p_2. The mean values of the relative location of the poles have also been calculated and are shown in Table 3. This averaging of estimated parameters over different subjects seems allowed, since the intersubject variations over one level are small in comparison to the variation of the parameters with background. However, we have to observe the necessary caution, since at the 100 Td level only three parameter sets are available, where one parameter set (JW) is derived from a data set which is rather noisy, and where the fit is not as good as one would like (see Table 1).

From Table 3 it can be seen that the (mean) ratio of the imaginary parts of the two poles is nearly independent of the background level, and so is the ratio of the real and imaginary parts of pole p_1. This means that α_1, β_1, and β_2 change by an equal amount if the background level is changed from 100 Td to 1200 Td.

Table 3. The relative location in the s-plane of the estimated parameters of the fourth-order linear filter. Seven subjects at 1200 Td and three subjects at a 100 Td background level. In all cases the stimulus diameter is 1 deg

	Background	α_1/α_2	β_1/β_2	$-\alpha_1/\beta_1$	$-\alpha_2/\beta_2$
JR74	1200	1.63	1.99	0.299	0.365
JAJR	1200	1.80	2.02	0.294	0.330
FB	1200	1.58	1.87	0.202	0.239
JP	1200	1.20	2.10	0.239	0.418
LT	1200	1.01	1.75	0.216	0.374
HD	1200	1.21	1.92	0.234	0.373
IH	1200	0.90	2.06	0.191	0.438
Mean	1200	1.33	1.96	0.239	0.362
LT	100	0.796	2.11	0.295	0.782
HR	100	0.923	2.09	0.221	0.501
JW	100	0.858	2.01	0.174	0.409
Mean	100	0.857	2.07	0.230	0.564

The ratio α_1/α_2 and $-\alpha_2/\beta_2$ changes with background, so it appears that this parameter α_2 does not change by an equal amount as do the parameters α_1, β_1, and β_2. Indeed, this should be the case if α_2 is independent of the background level, as was argued before.

In Fig. 2C all invariances in the parameters over the two background levels are illustrated in the pole-zero plots of subject LT at 100 and 1200 Td. The relative location of p_1 is approximately constant: for the two background levels the poles p_1 are (roughly) located on a straight line through the origin. For subject LT the ratio of the frequencies β_1 at 1200 and 100 Td and idem for β_2 is in the mean about 1.8.

The observed shift in parameters is slightly different from the isomorphy assumption (Roufs 1974a). This is shown in Fig. 3. The estimated impulse response of the 1200 Td level is plotted together with a scaled version (isomorphy assumption) of the estimated 100 Td impulse response. For the latter the time axis has been scaled by a factor 1.8. This means that all parameters associated with this scaled version are the 100 Td parameters multiplied by a factor 1.8. Thus the scaled parameters α_1, β_1, and β_2 of the 100 Td impulse response virtually coincide with those of the 1200 Td level but the parameters α_2 and z for these both cases significantly differ. From Fig. 3 it can be seen that the effect on the impulse response as a consequence from the shift that is found from our analysis is close to an isomorphic change. The difference in the impulse responses is that the one estimated at 1200 Td has a first negative phase that is broader and slightly deeper, and that the second negative phase is deeper than the scaled version of the 100 Td level. This implies that the estimated filter has more the character of a bandpass filter at the higher level.

In this way a comparison of results from parameter estimations of impulse responses can give insight into the changes of the linear filter with background level. It appears that the change in the parameters of the linear

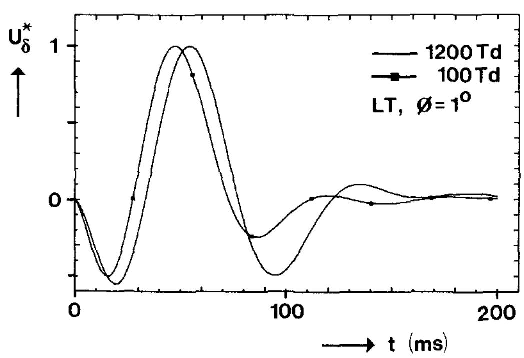


Fig. 3. The estimated impulse responses of subject LT for a 1 deg field at 100 and 1200 Td. The time axis of the 100 Td impulse response is scaled with a factor 1.8 (see text)

can be described by one multiplication factor only. The multiplication factor affects only three ($\alpha_1, \beta_1, \beta_2$) of the five parameters, the others (α_2, z) are independent of level. This, however, has been established only for a change of background level from 100 to 1200 Td. On the other hand, the shift in the parameters may well reflect the general change of the parameters of the linear filter for any change in background level.

5 Changes in Estimated Parameters with Variation of Field Size

The data that are available for different field sizes consist of impulse responses of two different subjects at

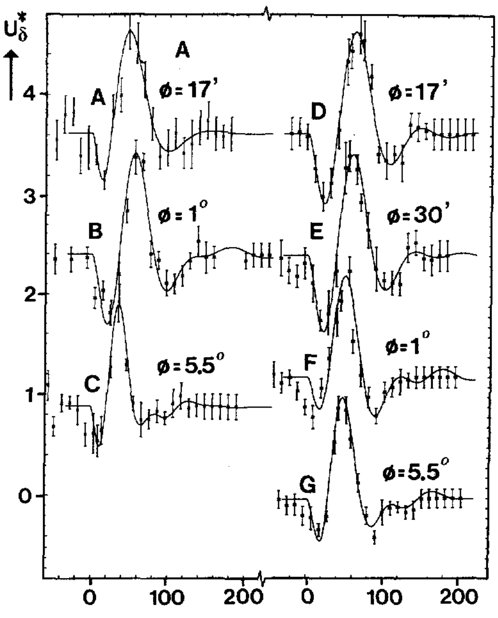


Fig. 4. Measured and estimated normalized impulse responses U_δ^* at 1200 Td for HD (Figs. A, B, and C are for field sizes 0.28, 1.0, and 5.5 deg, resp.) and IH (Figs. D, E, F, and G are for field sizes 0.28, 0.50, 1.0, and 5.5 deg, resp.). For representation purposes, all the figures except G are shifted along the vertical axis

1200 Td. Subject HD measured three impulse responses for field diameters of 0.28, 1, and 5.5 deg. From subject IH we have four impulse responses for field sizes of 0.28, 0.50, 1.0, and 5.5 deg. The impulse response data and estimates are shown in Fig. 4. All these impulse responses are triphasic, and as a general trend it can be seen that for larger field sizes the impulse responses become slightly faster.

The estimated parameters are shown in Table 4. The estimated parameters of subject HD for a field with a diameter of 0.28 deg were extremely unreliable. It was not possible to obtain variances and covariances of the estimated parameters. The results of the estimation process of the two subjects are also shown in Fig. 5 as confidence regions of the parameters in the s-plane. From Table 4 we see that the pole p_2 with the smallest norm is estimated to be almost equal over these field sizes for each subject. This is also reflected in Fig. 5, since the estimated (co-)variance regions of the pole p_2 all overlap. The other parameters vary with the field diameter. The pole p_1 moves approximately on a straight line parallel to the imaginary axis; the estimated frequency parameter β_1 decreases with decreasing field size. From Table 4 and Fig. 5 it can be seen that there is also a change in the parameter z with field size. This change in z is not as easily portrayed as is the case with β_1 since there seems to be no monotonous relation between this parameter and field size.

The conclusion we draw from this is that only part of the behaviour of the processing in the transient system is dependent on the spatial configuration of the stimulus. More specifically: the part of the processing of a linear filter that has spatiotemporal properties is reflected in the parameters $p_1 = \alpha_1 + j\beta_1$ and z.

6 Relation with Other Experimental Data

We want to compare the results we obtained from the analysis of the shifts in the parameters of the fourth-order linear filter with other psychophysical data. An obvious choice is to look at the De Lange curves that have been given in the literature many times. However,

Table 4. Estimated parameters of the fourth-order linear filter. Subject HD at 1200 Td and stimulus diameter 0.28, 1, and 5.5 deg. Subject IH at 1200 Td and stimulus diameter 0.28, 0.50, 1.0, and 5.5 deg

	Diam. (°)	α_1 (s^{-1})	β_1 (rad/s)	α_2 (s^{-1})	β_2 (rad/s)	z (s^{-1})	A ($10^4 s^{-2}$)	NF ($Td^{-1}s^{-1}$)
HD	0.28	−72.9	77.3	−36.9	58.6	47.7	−2.36	0.15
HD	1.00	−23.3	99.8	−19.3	51.8	11.8	−1.13	0.44
HD	5.50	−34.6	150.0	−31.0	62.9	63.1	−2.01	1.01
IH	0.28	−23.5	82.7	−31.4	42.5	15.3	−1.19	0.21
IH	0.50	−23.8	91.2	−25.9	48.4	9.64	−1.23	0.38
IH	1.00	−19.8	103.0	−22.0	50.2	53.8	−0.833	1.01
IH	5.50	−24.5	115.0	−23.2	51.9	44.8	−1.17	2.07

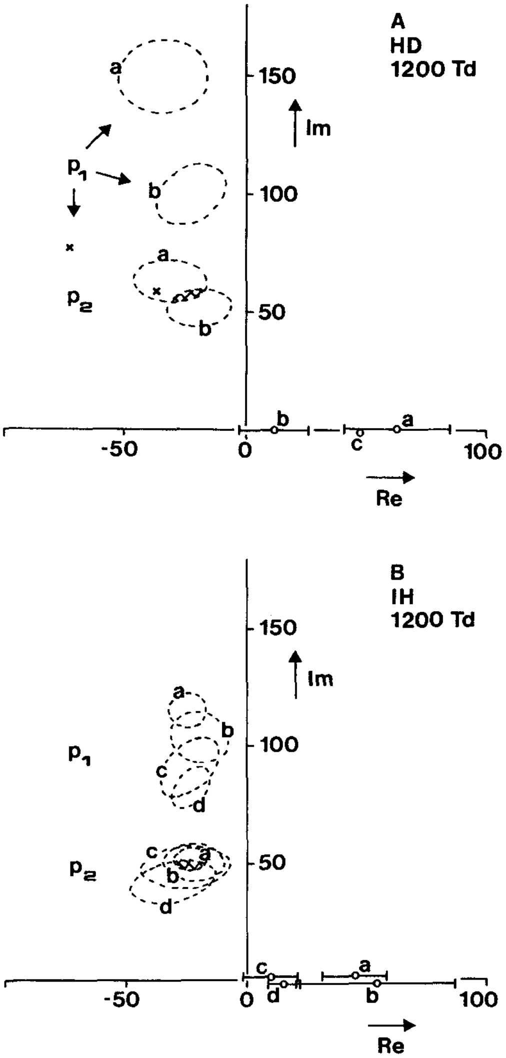


Fig. 5A and B. Pole-zero plots in the complex plane. Horizontal and vertical axes are the real and imaginary axes, respectively. The units are in s^{-1}. The lower part of the s-plane is not shown in this plot. The ellipses give estimates of the 90% confidence regions of the poles. The estimated poles are located in the centres of the ellipses. The zeros are indicated by a small circle and the bars give the 90% confidence intervals. **A** Subject HD, 5.5 (a), 1 (b), and 0.28 (c) deg field. **B** Subject IH, 5.5 (a), 1 (b), 0.50 (c), and 0.28 (d) deg field. For subject HD and a 0.28 deg field it was not possible to estimate reliable confidence regions; in this case the poles are given by crosses and the zero is indicated by a small circle denoted c

we do have to make several remarks. The first is that we do not have the De Lange curves for the same objects as those for whom the impulse responses were measured. Second, the amplitude spectrum of the Fourier transform of the estimated impulse response cannot be compared directly with a De Lange curve. In measuring a De Lange curve the experiment necessarily incorporates a stochastic effect. The detection of a sinusoid that is slowly switched on and off has a probability of being seen at each peak of the sinusoid. This will cause a lowering of the threshold because of "probability summation" (Roufs 1974b; Quick 1974). To account for the probability summation the noise of the system has to be modelled, and the exact circumstances of the De Lange measurement have to be known. Furthermore, the De Lange characteristic will be an envelope of the frequency characteristics of the sustained and transient channel operating in parallel. The transient system is the highest tuned filter, so the high frequency side of the De Lange curve should be comparable with the amplitude spectrum of the Fourier transform of the estimated impulse response, after correction for the probability summation. Because of the above remarks the comparison of the estimated filters with the De Lange curve can be qualitative only.

It is well known (Kelly 1971a; Roufs 1972a) that the De Lange curves change to a higher peak and cut-off frequency at higher luminance levels. In Fig. 6A several De Lange curves are shown with the background level as parameter (from Roufs 1972a). The same behaviour is found in our estimates, too. Figure 6B shows the amplitude gain spectrum of the Fourier transform of the impulse responses of LT at 100 Td and 1200 Td. The vertical axis is not arbitrary but scaled according to the sensitivity (the norm factor NF) of the transient system to an impulse for both levels. An increase in background level results in a lower sensitivity, a higher peak frequency and a higher cut-off frequency in both Fig. 6A and B.

Except for the low frequency side, which we cannot compare with the simulation from our model, as argued before, the effect of the variation of the field size on the De Lange curve is similar to the effect of the changing parameters of the impulse response as we have found (see Fig. 7). An increase in field size changes the temporal characteristics to a higher sensitivity, a higher peak and a higher cut-off frequency (Roufs and Bouma 1980). This is the same as is found in our analysis: the parameter p_1 changes to a higher norm, the impulse response is faster (see Fig. 4) and the measured sensitivity to an impulse response is higher for more extended fields (see norm factors NF in Table 4).

There is a qualitative difference between the amplitude spectrum of the proposed linear filter and the De Lange curves. The slope for high frequencies of the De Lange curves is steeper than the slope (0.9 log units/octave) in the linear model (1). Another difference between the De Lange curves and the calculated Fourier transforms at different background levels is that the high frequency asymptotes of the De Lange curves coincide. In the Fourier transform there is a

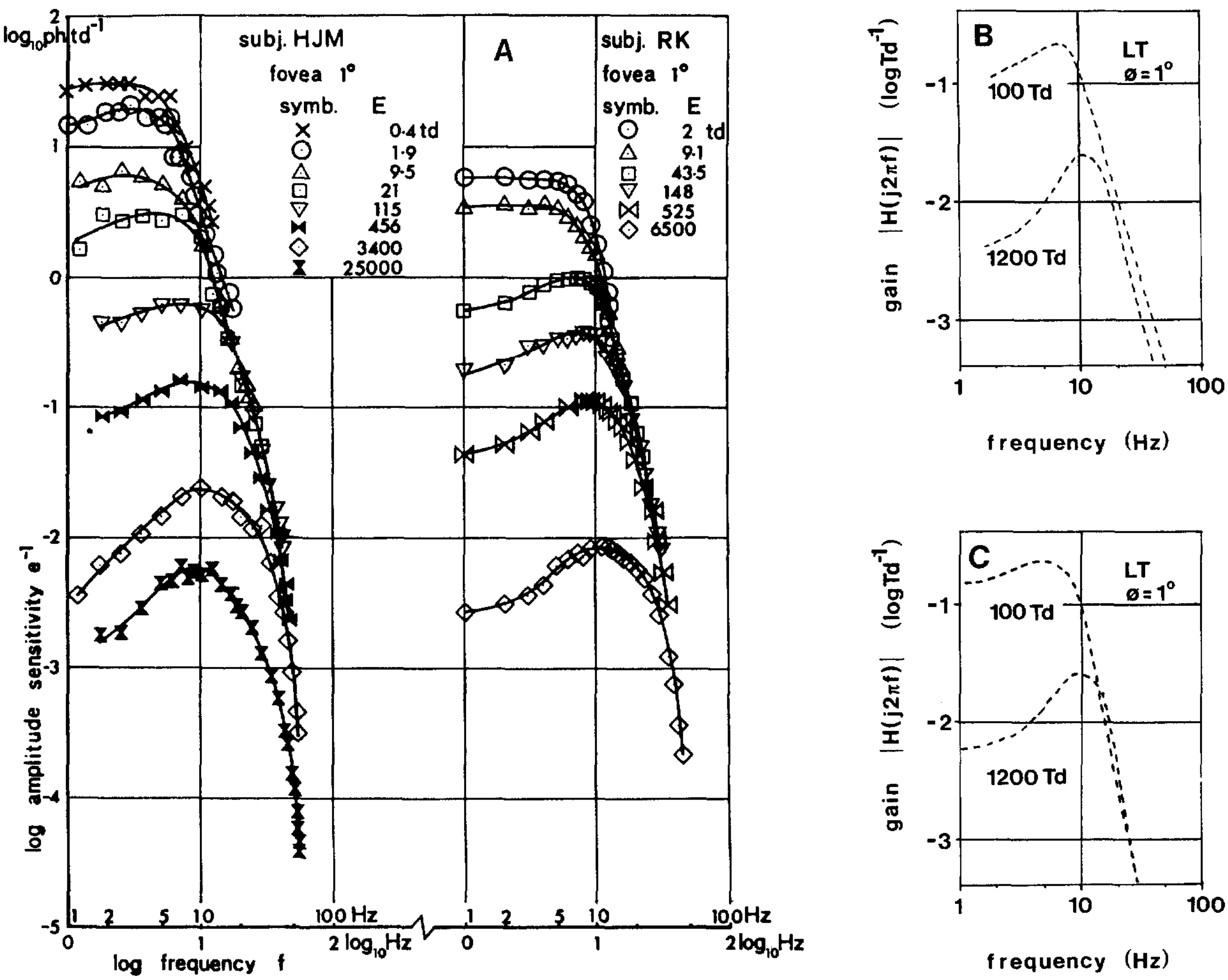


Fig. 6. A De Lange curves at different background levels for two subjects. Reprinted with permission from Vision Research 12, J. A. J. Roufs, Dynamic properties of vision. I. Copyright 1972 Pergamon Journals Ltd. **B** Amplitude spectrum of the Fourier transform of the impulse responses of LT at 100 Td and 1200 Td. The vertical axis is not arbitrary but scaled according to the sensitivity of the transient system to an impulse at these two levels. **C** The amplitude spectra of the estimated impulse responses of subject LT (1 deg field) at 100 and 1200 Td. The amplitude spectra of the estimated impulse responses of subject LT (1 deg field) at 100 and 1200 Td. The amplitude spectra of the estimated impulse responses (Fig. 6B) are both multiplied by the amplitude transfer function of a second-order filter (see text)

difference in height of about 0.5 log units between the high frequency asymptotes for the 100 and 1200 Td levels. There are several reasons why a steeper slope was not incorporated in our model. First of all the impulse responses to which the linear filter is fitted is adequately described by the fourth-order filter. To take more parameters into account would be contradictory to the parsimony principle. Furthermore, it would probably mean introducing ill-conditioned parameters in our estimation process.

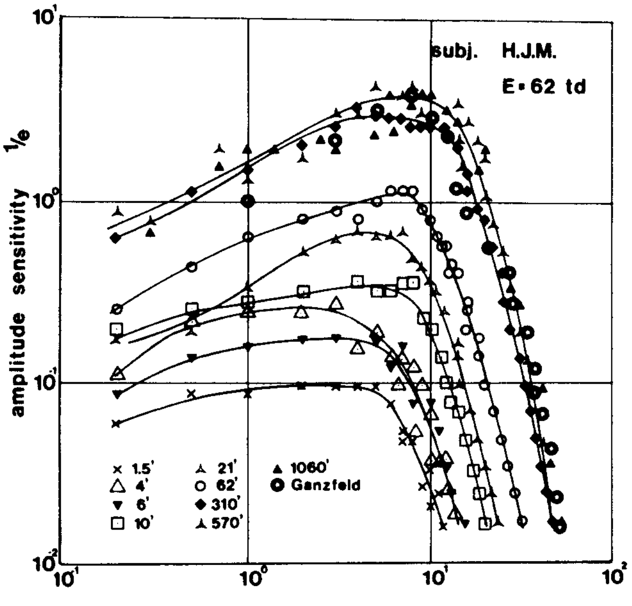
However, there is a simple way of changing the linear filter (1) such that it fits the De Lange curves. In Fig. 6C the Fourier transforms from Fig. 6B are multiplied by a second-order process,

$$G(s)=\frac{p_3^2}{(s-p_3)^2}\,. \tag{9}$$

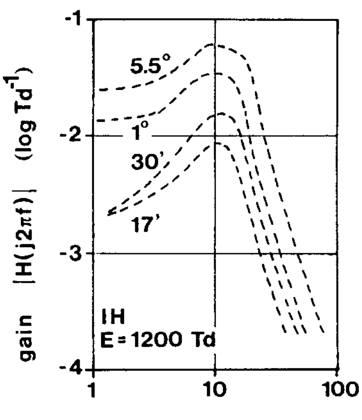
For the 1200 Td level we took $p_3=100\ \mathrm{s}^{-1}$ and for the 100 Td level we scaled p_3 down by the same factor as in p_1, namely 1.8 (see Sect. 4). The value of the pole p_3 is not critical at all. It should be somewhere above the peak of the Fourier transforms of Fig. 6B. Consequently, the two curves coincide for high frequencies (see Fig. 6C). The high frequency fall-off in Fig. 8 is now the same as was found experimentally, about 1.5 log units/octave (Kelly 1971a; Roufs 1972a). The estimated impulse response will hardly change after introducing this extra second-order process, since only the high frequency end (above the cut-off frequency) of the gain characteristic is modified. In the time domain the impulse response $g(t)$ of this extra filter is given by

$$g(t)=\mathscr{L}^{-1}\{G(s)\}=p_3^2 t\exp\{p_3 t\}\,, \tag{10}$$

where $\mathscr{L}^{-1}$ denotes the inverse Laplace transform.



a



b

Fig. 7. A De Lange curves for different field diameters at a background of 62 Td, from Roufs and Bouma (1980). Permission for reprint, courtesy Society of Information Display. **B** Amplitude spectrum of the Fourier transforms of the estimated impulse responses of IH at 1200 Td for four different field sizes: from bottom to top 17′, 30′, 1°, 5.5°. The vertical axis is not arbitrary but scaled according to the sensitivity of the transient system to an impulse for these field sizes at 1200 Td

Other experimental data that are consistent with the estimated impulse responses are threshold measurements of pulses with variable duration (Blommaert and Roufs 1987; den Brinker and Roufs 1989) and the experimentally determined phase characteristic. The phase characteristic has been measured by a subthreshold summation technique and showed a linear phase relation for a 1 deg field at 1200 Td for frequencies from 1 to 25 Hz (Roufs et al. 1984). The estimated parameters of the fourth-order filters are such that they give an approximately linear phase for that frequency range (see Appendix).

In conclusion we can state that the effects of background and field size variation are qualitatively the same in De Lange curves, impulse response measurements and in the estimated parameters of the fourth-order linear model. From the estimated parameters of our model we see that the effect of an increase in background level and an increase in field sizes has quite a different effect on the estimated parameters.

7 Discussion

In Sect. 2 our choice for the model was given. It was hoped that the filter (1) would give a good description of the available data, but also that it would allow us to obtain insight into the temporal processing within the transient channel. However, the choice was also founded on its common usage in engineering and its convenient mathematical formulation. It does not rule out the possibility that filters other then (1) can provide descriptions of the experimental data that are equally well, nor do we think that the observed shifts in the parameters is exclusively reserved to the choice of damped sinusoids as fundamental functions.

We have shown that the subthreshold measurements of the impulse response of the transient visual system can be adequately modelled in a fourth-order linear filter with two complex pole pairs and one zero in its transfer function. From this representation of the measured impulse responses predictions of the response of the system can be made for other stimuli (Blommaert and Roufs 1987). But more important is that these fourth-order filters give insight into the processing of stimuli in the transient channel of the visual system for different mean luminance levels and different spatial configurations.

On the basis of the systematic parameter changes, we are able to propose a model for the transient system which provides an approach towards a description of the spatiotemporal processing. The model is shown in Fig. 8, and is spatiotemporal in nature. It consists of two processing stages. The first step is a linear spatiotemporal filter L_1. This filter is not only dependent on the mean luminance E, but also on the spatial configuration, which we describe by its spatial frequency w. This is denoted as

$$L_1 = L_1(E, w)\,. \tag{11}$$

For the parameter p_1 which describes this filter L_1 the shift in the parameter caused by background variation and by field size variation can be separated, at least in a

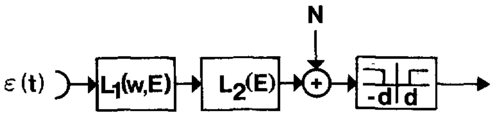


Fig. 8. Proposal for a spatiotemporal model, based on analysis of changes in estimated parameters from a fourth-order model that is fitted to subthreshold measurements of impulse response. The filter L_1 is dependent on both mean luminance E and spatial characteristics of the stimulus, while the filter L_2 is dependent on the mean luminance only. The spatial dependence is denoted by w, the spatial frequency of the stimulus. The last stage is formed by a detector with threshold d

first-order approximation:

$$p_1(w,E)=\hat{p}_1(w)f(E), \tag{12}$$

where $f(E)$ is a real valued function of the mean luminance E, and $\hat{p}_1$ is the value of p_1 for $f(E)=1$. The separability of the effect of the mean luminance and field size was shown in our analysis for a 1 deg field only. However, such separability will probably exist for field sizes near 1 deg where the transient activity is dominant and which is, therefore, very attractive from a modelling point of view.

The parameter z, the position of the zero, changes with field size, so this parameter should be incorporated in the spatiotemporal filter L_1. The complicating factor for this parameter is that there is no monotonous change with field size, as was observed for p_1.

The second step is a purely temporal linear filter L_2. In the transfer function (1) this filter is reflected in the pole p_2, the pole with smallest norm. This pole is dependent on the mean luminance only. We denote the dependence as

$$L_2=L_2(E), \tag{13}$$

where the mean luminance level is given by E.

The refinement of the fourth-order model, i.e. the introduction of a third stage characterized by p_3, can be easily incorporated in Fig. 8. It was shown that p_3 changes with background level in the same way as p_1. Whether and how p_3 should change with field diameter, and consequently whether it belongs to L_1 or L_2, is something as yet to be explored.

For the spatiotemporal filter L_1 it is possible to construct a distributed electrical network as has been done in several studies for the electrical coupling between retinal cells (Bennet 1977; Torre et al. 1983). It was found that pole p_1 changes in such a way with field size that for larger fields the filter L_1 has a "faster" impulse response. This corroborates the physiological findings of Detwiler et al. (1980), who found this for the rods in the retina of the snapping turtle. Possibly the filter L_1 is located in the retina. We hope to explore the possibilities of translating the foregoing behaviour of the poles and zeros with spatial extension into the behaviour of a linear distributed electrical network elsewhere.

In conclusion, we have analysed the behaviour of poles and zeros of linear filters that were fitted to impulse responses obtained under different experimental conditions. On the basis of the shifts that are observed in the poles and zeros upon a change in experimental conditions it is possible to obtain insight into the operation of the transient visual system. From our analysis a spatiotemporal model for the transient system evolved (Fig. 8). The main features of this model are linearity, simplicity, and parsimonious use of parameters. Also it was shown that changes in background level and spatial extension of the stimulus have strikingly different effects on the parameters of the model, and that these two effects are probably separable. The model is in agreement with physiological data. As a consequence of the simplicity of the model, it is suitable for detailing. This was shown by making a small modification such that the model matches the De Lange curves.

Appendix: Approximation of a Linear Phase Characteristic

Consider the fourth-order filter given by (1). The zero z is assumed to be located in the right-half plane, the amplification factor A is assumed to be negative (see Table 2). We define the phase ϕ by

$$H(j\omega)=|H(j\omega)|\exp\{j\phi(\omega)\}.$$

The phase ϕ is split into three parts:

$$\phi=-\phi_0-\phi_1-\phi_2,$$

where

$$\phi_0=\arctan\left(\frac{\omega}{z}\right),$$

$$\phi_1=\arctan\left(\frac{\omega-\beta_1}{-\alpha_1}\right)+\arctan\left(\frac{\omega+\beta_1}{-\alpha_1}\right),$$

$$\phi_2=\arctan\left(\frac{\omega-\beta_2}{-\alpha_2}\right)+\arctan\left(\frac{\omega+\beta_2}{-\alpha_2}\right).$$

The phase ϕ_i for $i=0,1,2$ can be approximated by linear line pieces according to

$$\arctan(\gamma)=\gamma, \qquad |\gamma|\leqq\tfrac{\pi}{2},$$

$$\arctan(\gamma)=\mathrm{sgn}(\gamma)\tfrac{\pi}{2}, \qquad |\gamma|>\tfrac{\pi}{2},$$

where sgn denotes the sign of a variable. To obtain a linear phase ϕ for low frequencies in the first-order approximation of the phases ϕ_i the parameters (α_i, β_i, z) with $(i=1,2)$ are dependent according to

$$z=-\alpha_1=-\alpha_2, \tag{14}$$

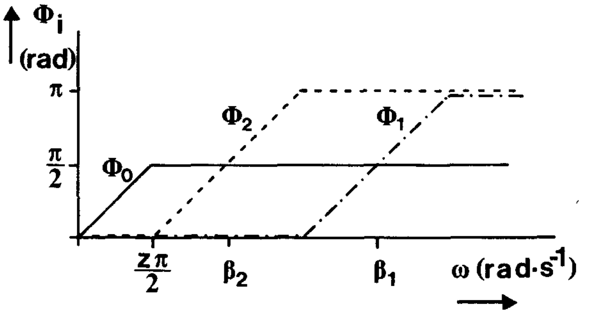


Fig. 9. The phases ϕ_i ($i=0,1,2$) of the fourth-order filter approximated by linear pieces (see text)

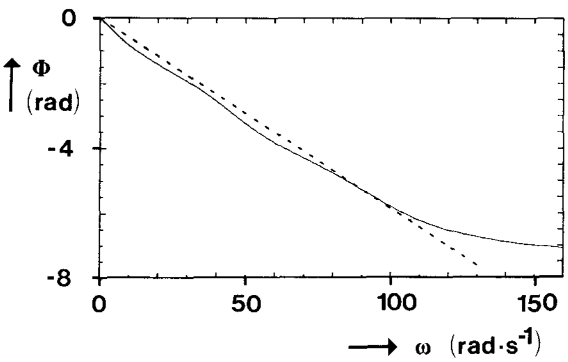


Fig. 10. The estimated phase characteristic of subject JP (1 deg field, 1200 Td). The parameters of the fourth-order filter are given in Table 1. The straight line depicts the relation ωt_{ex}

which ensures that all slopes in the first-order approximation of the phases ϕ_i are equal, and

$$\frac{\beta_2}{-\alpha_2} = \frac{\beta_1}{-2\alpha_1} = \pi, \tag{15}$$

which results in a ϕ that is linearly dependent on ω (with a slope z^{-1}) over the largest possible range. The first-order approximations to the phases ϕ_i are shown in Fig. 9 and it is easy to see that with the above mentioned relation between the parameters a linear phase ϕ is obtained (within this approximation).

From Table 2 we see that the phase characteristic of the fourth-order filter at 1200 Td and a 1 deg field is close to a first-order approximation of a linear phase for low frequencies. For other conditions (than 1200 Td and 1 deg field) this is not so. In Fig. 10 the phase characteristic of subject JP (1200 Td, 1 deg field) is plotted with the parameters from Table 2. We see that the estimated phase is indeed close to a linear phase characteristic. The dotted line in the Fig. 10 is the line ωt_{ex} where t_{ex} is the time of the occurrence of the extremum of the estimated impulse response. This line and the phase characteristic are very close. This is in accordance with the measurements of the phase characteristic as performed by Roufs et al. (1984).

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