

Temporal impulse and step responses of the human eye obtained psychophysically by means of a drift-correcting perturbation technique

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TEMPORAL IMPULSE AND STEP RESPONSES OF THE HUMAN EYE OBTAINED PSYCHOPHYSICALLY BY MEANS OF A DRIFT-CORRECTING PERTURBATION TECHNIQUE*

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Abstract—Internal impulse and step responses are derived from the thresholds of short probe flashes by means of a drift-correcting perturbation technique. The approach is based on only two postulated systems properties: quasi-linearity and peak detection. A special feature of the technique is its strong reduction of the concealing effect of sensitivity drift within and between sessions. Results were found to be repeatable, even after about one year. For a 1° foveal disk at 1200 td stationary level, impulse responses of increments and decrements were found to be mirror-symmetrical. They were equal to the derivatives of the measured step responses. As a consequence the threshold of any fast-changing retinal illumination should be predictable. This will be tested in a subsequent paper. The transfer function of the system responding to a 1° stimulus shows a band-pass filter type of processing for transients, confirming quantitatively earlier findings. In contrast, a foveal point source on an extended background of 1200 td, to which impulse and step responses appear also to be linearly related, gives rise to low-pass filter action of the system.

INTRODUCTION

This paper concerns the dynamic processing of visual stimuli near threshold level. In order to be able to predict thresholds of a fairly large class of time dependent stimuli, dynamic properties of the system have to be identified and the related parameters specified. The latter is usually done by deriving some basic response function from measurements. Several examples of this systems analysis kind of approach can be found in literature (De Lange, 1952; Veringa, 1961; Kelly, 1961, 1969; Matin, 1968; Levinson, 1968; Sperling and Sondhi, 1968; Hallett, 1969a,b; Rashbass, 1970; Kelly and Savoie, 1978).

In an earlier series of papers one of the present authors constructed such a model in two steps of refinement (Roufs, 1971; 1972a, b; 1973; 1974a, b, c). In these cases the basic response function was obtained by the thresholds of sinusoidal modulation and related to the thresholds of various types of one shot functions and perception latency. The results could be explained by the assumption of two systems operating in parallel (Fig. 1). A low-pass filter, associated with the physiologically defined "sustained" cells (Cleland *et al.*, 1971) and a strict band-pass type of filter associated with "transient" cells. In the case of sinusoidal modulation the output of the former was suggested to cause the homogeneous brightness variations at low frequencies ("swell") and the typical percept seen at the high frequencies ("agitation"). The bandpass filter was found to process quasi-linearly and an impulse response was derived from the gaincurve by assuming

minimum phase behaviour (but for a pure time delay). This impulse response was used to calculate the response of other transients by convolution from which their thresholds could be calculated.

Impulse responses or any response, however, can theoretically be derived from threshold measurements in a more direct way on the basis of quasi-linearity and peak detection by applying a special case of sub-threshold summation, *perturbation*. This involves measurements of changes in threshold of a *probe*-

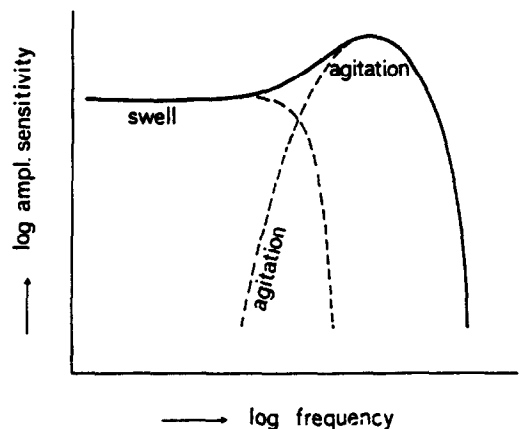


Fig. 1. Schematic representation of the amplitude sensitivity curves of harmonically modulated light of a 1° -foveal field as a composite of the curves of two constituent processes and the perceptual phenomena associated with the two output variables. Homogeneous brightness changes ("swell", Roufs, 1972a, 1974a) are linked with a low-pass filter or sustained type of processing. The typical inhomogeneous percept accompanying flicker at middle and high frequencies ("agitation") is connected with a linear band-pass filter or transient type of processing.

* Presented at the European Conference of Vision 1979, Noordwijkerhout.

flash, the response to which is superimposed on the testflash response. In practice the derivation of responses from changes in a small quantity, as thresholds usually are, is hampered seriously by imprecision due to non-stationary effects like drift in the thresholds themselves. Fortunately, as will be explained below, this disadvantage can be overcome by a special driftcorrecting measuring technique, using a sensitivity reference all the time.

An important additional advantage of the use of a probe flash is that the perceptual attribute to be detected is the same for all kinds of test stimuli since the only stimulus the response to which exceeds the critical value to be detected is that of the probe flash.

Furthermore, in interpreting the results obtained with one short probe flash, no substantial corrections for probability summation have to be made, as are necessary for instance for prolonged stimuli like gated sinusoids (Roufs, 1973; 1974c).

In order to facilitate comparison, most experiments were performed with the same stimulus configuration and background levels used in previous experiments mentioned above.

In this article it will be shown that:

(i) Transient responses of the visual system can be measured by means of a drift-correcting perturbation method within sufficient precision to make quantitative analyses applicable.

(ii) The results can be understood on the basis of quasilinearity and peak detection, which can be tested in combination.

(iii) The system is found to react as a band-pass filter upon fast changes of luminance in the case of a foveal stimulus. However, in the case of a point source the system behaves as a low-pass filter.

In a subsequent article it will be shown that thresholds of several types of transients can be predicted accurately and simply from the impulse response obtained in this way. (A short report of some essentials was published before, Roufs and Blommaert, 1975).

METHODOLOGICAL CONCEPTS

A model

Changes of retinal illumination caused by a stimulus on a steady background level E will be described by $\epsilon_f f(t)$, ϵ_f being the amplitude factor and $f(t)$ the normalized time function. In this article we shall only consider small and fast changes of retinal illuminance (transients). For sufficiently large fields these evoke perceptual changes in the visual field ("agitation") which cannot be identified as brightness changes. For small fields, on the other hand, clear brightness increments or decrements may be observed. The model used is illustrated in Fig. 2.

Two deterministic systems properties are postulated. First, small changes are processed linearly:

$$L\{\epsilon_f f(t)\} = \epsilon_f U_f(t), \quad (1)$$

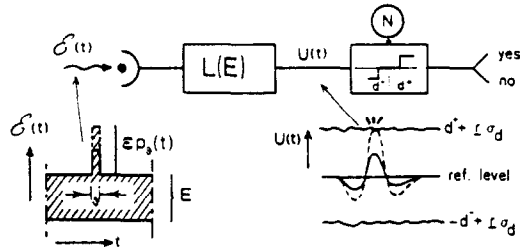


Fig. 2. The working of the hypothetical mechanism for detecting fast luminance variations. At the lower left an example of such a variation of retinal illumination is shown. The signal, which is proportional to a (small) luminance variation, is processed linearly by the first part L of the system. Response $U(t)$ leads to perception if the deviation from the stationary state exceeds a certain amplitude d^+ or $-d^-$. r is the standard variable of the stochastic process.

where L is a linear operator and $U_f(t)$ the response from the linear system to $f(t)$. Second, the stimulus $\epsilon_f f(t)$ is seen if its response deviates at least by a magnitude a from the stationary reference level (peak detection). This might be a signal-to-noise criterion or an internal threshold level. Thus at threshold:

$$\epsilon_f \text{extr} \{U_f(t)\} = a \quad (2)$$

$$a = d^+ \text{ or } -d^-; d^+, d^- > 0.$$

If the extremum happens to be positive $a = d^+$, otherwise $a = -d^-$ (symmetry can be concluded within the model from earlier experiments (Roufs, 1974), but it is not a necessary condition for the following). Equation (2) states that if $U_f(t)/a$, the response to $f(t)$ expressed in a units is known, the threshold value of the amplitude factor ϵ_f can be calculated. The magnitude d is in fact thought to be a stochastic variable, giving rise to the psychometric function and involving some interesting invariances (Roufs, 1974c). In this article, however, the intrinsic stochastic properties are not essential and therefore d will be treated for convenience as a deterministic quantity unless specified otherwise. In a subsequent paper the effect of stochastic variations of d will be dealt with in detail in connection with stimuli for which it is relevant (this model differs from the one proposed by Rashbass, 1970. However, it predicts the ellipse like figures as will be shown in full detail further on).

For all stimuli the values ϵ_f corresponding with a 50% detection probability will be taken as threshold.

As an example, let us take a rectangular flash with an intensity increment ϵ and a duration θ which is short compared to the time constants of system L . Denote this flash by $\epsilon p(t)$. From its response, $\epsilon U_p(t)$, we obtain the threshold value by applying equation (2):

$$\epsilon_p \text{extr} \{U_p(t)\} = a. \quad (3)$$

The system L is fully characterized by its unit impulse response $U_\delta(t)$. If the flash is short, the response $\epsilon U_p(t)$ can be approximated by $\epsilon_p \theta U_\delta(t)$. The threshold

condition becomes in this case:

$$\epsilon_p \theta \text{extr} \{U_d(t)\} = \epsilon_p \theta U_d(t_{ex}) = a, \quad (4)$$

where t_{ex} is the time after stimulus onset at which $U_d(t)$ attains its extreme value. Thus, at threshold, stimulus factors are related to the extreme of the impulse response by:

$$\frac{1}{\epsilon_p \theta} = \frac{U_d(t_{ex})}{a}. \quad (5)$$

The right-hand side of the equation will be referred to later on as the norm factor of the unit impulse response.

In order to predict thresholds of arbitrary fast changing stimuli by means of equation (2), not $U_d(t_{ex})/a$ but $U_d(t)/a$ is generally needed, because the response to an arbitrary time function $\epsilon_f f(t)$ is given by

$$\epsilon_f L\{f(t)\} = \epsilon_f \frac{U_f(t)}{a} = \epsilon_f \int_0^\infty f(t-\tau) \frac{U_d(\tau)}{a} d\tau. \quad (6)$$

Equation (6) is a convolution of the input with the impulse response.

Perturbation approach

As said above, perturbation is a method that can be used to determine responses from measured thresholds, based on the assumed linearity and on peak detection. The essentials of the method are shown in Fig. 3.

In order to probe the response to some stimulus unambiguously the response to the probe flash has to have one clear dominant phase which can trace the profile to be measured. (In Fig. 3 this would be the second phase.) If there is any doubt, this can be tested within the same theoretical frame (see Roufs, 1974a, p. 840). Now take a combination of a short flash

$\epsilon_p p_\theta(t)$ and any other test transient $\epsilon_f f(t)$, delayed some time τ , the response to which we want to determine. The threshold condition for the combination is:

$$\text{extr} \{ \epsilon_p \theta U_d(t) + \epsilon_f U_f(t-\tau) \} = a. \quad (7)$$

Since we want to probe the response to $\epsilon_f f(t)$ with the dominant phase of the probe flash response $\epsilon_p \theta U_d(t)$, we shall have to make sure that for any τ no other combination of the phases of probe and test response meet the amplitude criterion a . In mathematical terms:

$$|\text{extr} \{ \epsilon_f U_f(t) \}| \ll |\text{extr} \{ \epsilon_p \theta U_d(t) \}|. \quad (8)$$

In fact it is this inequality which characterizes perturbation as a special case of subthreshold summation. The condition prescribed by equation (8) is also determined by the stochastic nature of a and the necessity of keeping the joint probability of all other peaks negligible with respect to that of the dominant phase. This condition is especially relevant for prolonged stimuli. Thus, equation (7) simplifies to:

$$\epsilon_p \theta U_d(t_{ex}) + \epsilon_f U_f(t_{ex} - \tau) = a. \quad (9)$$

It is convenient to use a preset ratio $\epsilon_f/\epsilon_p = q$ (see Fig. 3). Then from equation (9):

$$\frac{\theta U_d(t_{ex})}{a} + \frac{q U_f(t_{ex} - \tau)}{a} = \frac{1}{\epsilon_p(\tau)}. \quad (10)$$

By measuring ϵ_p at various values of τ , the wanted function $U_f(t_{ex} - \tau)/a$ can be found in principle by plotting $1/\epsilon_p$ against $-\tau$. The varying second term in equation (10) is superimposed on the constant first term.

If the test stimulus is also a short rectangular flash of the same duration as the probe flash, equation (10) is simply:

$$\frac{U_d(t_{ex})}{a} + q \frac{U_d(t_{ex} - \tau)}{a} = \frac{1}{\theta \epsilon_p(\tau)}, q \ll 1. \quad (11)$$

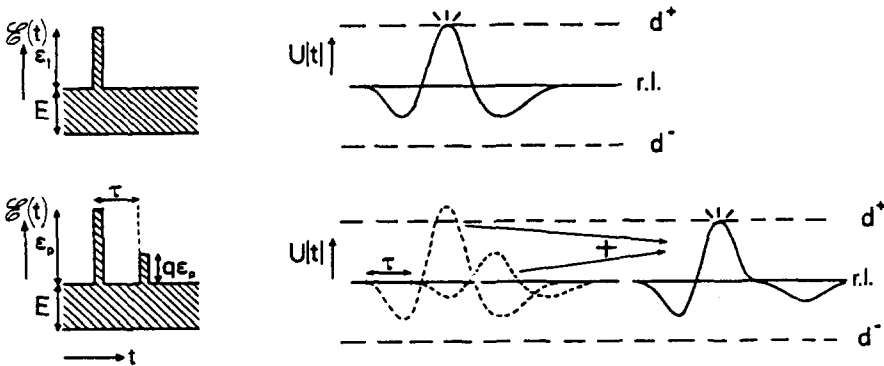


Fig. 3. The principles of perturbation. The upper left is a short rectangular flash, effectively an impulse. Upper right represents the response of system L at threshold condition. The lower left is the combination of probe flash and smaller test flash. In the lower right part, the interaction of the two individual responses (dashed curves) and the resulting response (continuous curve) at threshold condition are shown. Notice that in this case the intensity of the probe flash in the combination must be larger than in the case of one isolated flash, reflecting the influence of the test flash response.

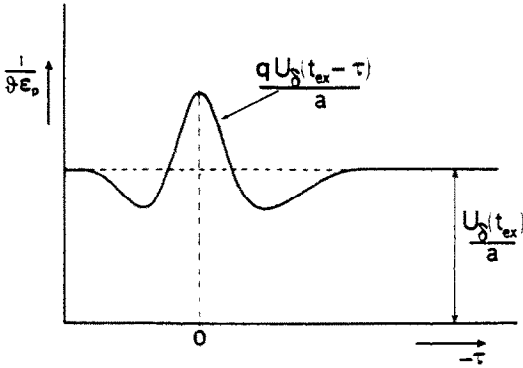


Fig. 4. Illustration of how the impulse response might be extracted from measurements following equation (10) if no sensitivity drift were to occur.

This is illustrated in Fig. 4. According to equation (11) there is a linear relationship between ϵ_p^{-1} and $U_d(t_{ex} - \tau)/a$. In practice, however, measuring the response according to equation (11) has one serious disadvantage. Apart from the intrinsic spread due to the sampling procedure in determining the 50% thresholds, there is also a slow and relatively large sensitivity drift within and between sessions. (This is reflected for instance in the drift of repeatedly

measured thresholds of a single flash, examples of which will be given later). Both drift in the amplitude criterion a (or the signal-to-noise ratio) and metabolically caused changes in $U_d(t_{ex})$ are likely candidates as a source of this drift. However, without loss of generality we shall attribute the drift to the former, stating,

$$a = a(t). \tag{11a}$$

Since it takes time to do the measurements, special precautions have to be taken against the concealing effect of these variations. This can be done by means of a sensitivity reference as will be shown below.

Two drift-correcting techniques

Two practical methods were investigated:

(a) *The "Slope" method.* Differentiating equation (11) with respect to q one obtains:

$$\frac{U_d(t_{ex} - \tau)}{a} = \frac{1}{\theta} \frac{\partial}{\partial q} \{ \epsilon_p^{-1}(\tau) \}. \tag{12}$$

The right-hand side contains only experimental values. In practice, a series of slightly different q values around $q = 0$ are used. Figure 5 illustrates the principle for each value of τ ; the value of $1/\epsilon_p$

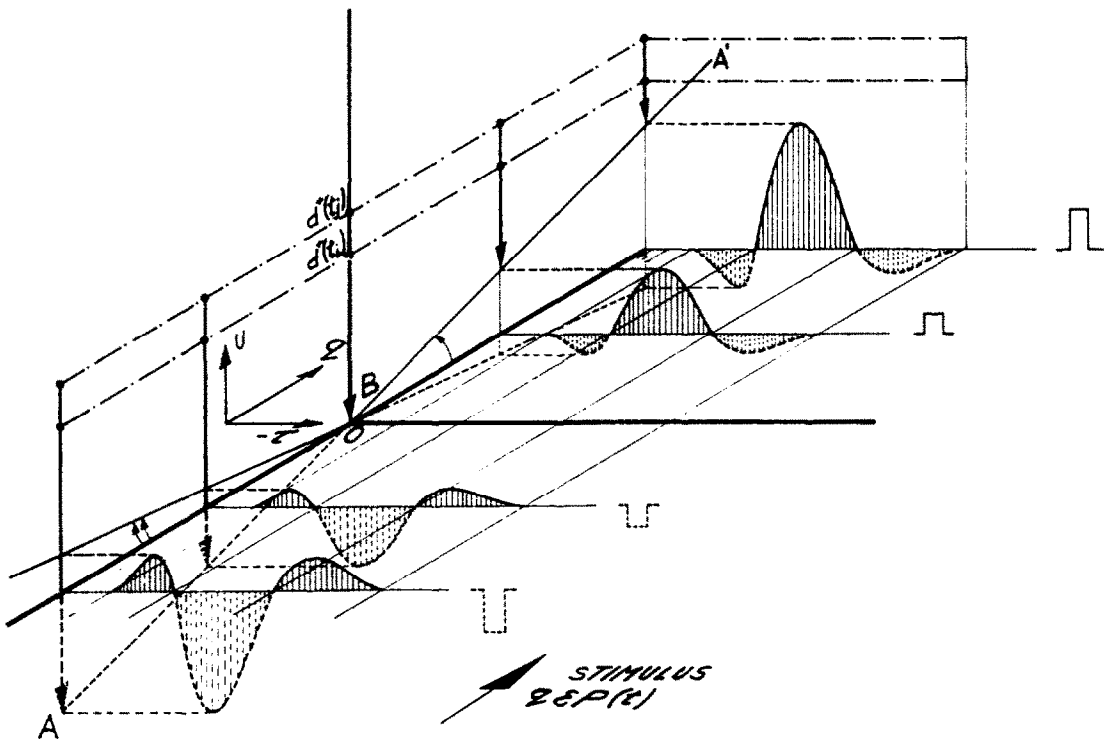


Fig. 5. Illustration of the "slope" method. The imaginary response of the system to various incremental or decremental short flashes, $q\epsilon_p(t)$, with a fixed probe-stimulus time interval. Negative q -values (see text) are associated with decremental flashes. The response amplitude at a fixed interval τ between probe and stimulus onset is probed at a time t_p with respect to the "amplitude ceiling" $d(t)$. The probing is symbolized by the arrows. The larger the amplitude of the response of the test stimulus at a given τ , the larger the slope found. If the measurements are repeated at a later time, t_p , the "ceiling" has been drifted upwards but the slope is not affected provided there is no considerable drift in the time needed to do the measurements.

determined in the shortest possible time interval $[t_i, t_i + \Delta t_i]$ are plotted against q . In Fig. 5 we are thus probing along line A - A'. Experimental data can be found in Fig. 9. If Δt_i is sufficiently small, drift can be neglected within this interval. From the slope of the line, $U_{\delta}(t_{ex} - \tau)/a(t_i)$ is calculated with equation (12). The norm factor of equation (5), using the intersection point $1/\epsilon_p$ at $q = 0$, serves as a reference. It represents the sensitivity at time t_i . In Fig. 5 this is symbolized by arrow B. In determining the shape of the response, the effect of drift can now be reduced substantially by normalizing equation (12) with the norm factor

$$U_{\delta}^*(t_{ex} - \tau) = \left[\frac{U_{\delta}(t_{ex} - \tau)}{a} \right]_{t_i} \left[\frac{a}{U_{\delta}(t_{ex})} \right]_{t_i} \\ = \frac{1}{\epsilon_p(t_i)} \frac{\partial}{\partial q} (\epsilon_p^{-1}). \quad (13)$$

After having finished the experiment for all chosen values of τ at different t_i 's, the absolute value of the impulse response $U_{\delta}(t_{ex} - \tau)/a$ can be estimated by multiplying U_{δ}^* by the norm factor averaged over all times t_i . In a manner of speaking we have shifted the effect of drift from the shape-determining procedure to the scale factor, where it hurts less and can be averaged out.

(b) *The "Method of Pairs"*. As a special case of the foregoing we usually used only two q -values, the accompanying probe flash thresholds being measured immediately after one another. The "fast pairs" have the advantages of a short execution time, symmetry in sampling strategy and simplicity of handling.

Their use will be elucidated only for the special case of an impulse response acting as a perturbation function. The derivation for the step response is analogous. For simplicity we will choose probe and test flash to have the same duration.

The formulas for any other type of perturbation can be derived along the same lines. Suppose we use two q -values $q\{q_1, q_2\}$. From equation (11) we obtain:

$$\frac{U_{\delta}(t_{ex})}{a(t_i)} + q_1 \frac{U_{\delta}(t_{ex} - \tau)}{a(t_i)} = \frac{1}{\theta \epsilon_{p1}} \quad (14)$$

and

$$\frac{U_{\delta}(t_{ex})}{a(t_i + \Delta t)} + q_2 \frac{U_{\delta}(t_{ex} - \tau)}{a(t_i + \Delta t)} = \frac{1}{\theta \epsilon_{p2}}. \quad (15)$$

If Δt is sufficiently small, then $a(t_i) \approx a(t_i + \Delta t)$. By elimination we obtain from equations (14) and (15):

$$\frac{U_{\delta}(t_{ex} - \tau)}{a(t_i)} = \frac{1}{\theta(q_1 - q_2)} \left(\frac{1}{\epsilon_{p1}} - \frac{1}{\epsilon_{p2}} \right). \quad (16)$$

The norm factor is:

$$\frac{U_{\delta}(t_{ex})}{a(t_i)} = \frac{1}{\theta(q_1 - q_2)} \left(\frac{q_1}{\epsilon_{p2}} - \frac{q_2}{\epsilon_{p1}} \right). \quad (17)$$

In order to obtain the response shape we again use the normalized expression, dividing (16) by (17):

$$U_{\delta}^*(t_{ex} - \tau) = \frac{\epsilon_{p1} - \epsilon_{p2}}{q_2 \epsilon_{p2} - q_1 \epsilon_{p1}}. \quad (18)$$

In practice it is often convenient to simplify further, for instance by taking $q_1 = q; q_2 = -q$, meaning that the test flashes of the pairs of combination are either an increment or a decrement flash of equal amplitudes. Then equation (16) simplifies to:

$$\frac{U_{\delta}(t_{ex} - \tau)}{a} = \frac{1}{20q} \left(\frac{1}{\epsilon_{p+}} - \frac{1}{\epsilon_{p-}} \right) \quad (16a)$$

where ϵ_{p+} and ϵ_{p-} are the thresholds of the positive and negative test flashes in combination with the probe.

Equation (17) becomes:

$$\frac{U_{\delta}(t_{ex})}{a} = \frac{1}{2\theta} \left(\frac{1}{\epsilon_{p+}} + \frac{1}{\epsilon_{p-}} \right) \quad (17a)$$

and equation (18):

$$U_{\delta}^*(t_{ex} - \tau) = \frac{1}{q} \left(\frac{\epsilon_{p-} - \epsilon_{p+}}{\epsilon_{p+} + \epsilon_{p-}} \right). \quad (18a)$$

The unit impulse response, $U_{\delta}(t_{ex} - \tau)/a$, can be found again by multiplying the normalized unit impulse response by the averaged norm factor.

The response $\epsilon_f U_f(t)/a$ of an arbitrary time function $\epsilon_f f(t)$ can be derived with the aid of equation (6), and its threshold ϵ_f can be predicted with equation (2).

It is clear that this method only functions properly if the 50% thresholds of the pair elements are measured consecutively and sufficiently fast to make the effect of drift negligible. This implies a limited number of trials for each psychometric function. Precision can be improved by repetition and averaging the data obtained after applying equations (13) and (18). The effect of residual drift in the time interval needed to determine the thresholds of the pairs can be decreased by measuring the repetitions in counter-balanced order. The use of a reference implies that data of normalized responses, obtained at different sessions, can be averaged.

The perturbation method has two consequences for the measured responses:

(a) The position of the response on the time axis relative to stimulus onset is not known, because all points are measured relative to t_{ex} .

(b) In the case of the large stimuli, where there is no difference between the perceptual attributes of incremental and decremental flashes at threshold, there is a mirror ambiguity of the response with respect to the zero axis, since a in equations (5) and (11) might be d^+ or $-d^-$, depending on the sign of the extremum of $U_{\delta}(t)$. For small stimuli the response peaks of incremental flashes may meaningfully be called positive since they always give rise to brightness increments.

APPARATUS AND PROCEDURE

Apparatus

The stimulus was either a centrally fixated circular field of 1° , having a dark surround or a foveal point source of $0.8'$ on an 11° background. It was seen in Maxwellian view through an artificial pupil with a dia of 2 mm, provided with an entoptic guiding system to check the centre of the pupil of the eye (Roufs, 1963). The light was generated by a linearized RCA glow modulator, operated around a suitable working point (13 mA). The luminance of the background was set by attenuating "the working point luminance" by means of a neutral filter. The modulation of the background luminance was controlled electronically by function generators. The amplitude of the desired function could be quickly adjusted with a dB step attenuator. The calibration of the dynamic stimuli was checked before every session by means of a photomultiplier tube, properly corrected with respect to spectral sensitivity. In the case of the point source superimposed on the background, the working point had to be taken very low in spite of a heavy neutral filter. Consequently the light had to be monitored continuously in order to correct for temperature effects. The colour was practically white. The background level was kept constant by keeping the working point current constant during the session. Its light output was checked before and after each session. The ratio q between test and probe flash, when applying perturbation (see Methodological concepts), was set in the way shown in Fig. 6.

The subject had a knob to release the stimulus, which was delayed for a convenient time interval. The beginning of stimulus was marked by an acoustic signal. Three buttons enabled him to answer with "yes", "no" or "rejection" (when, for instance, the subject had blinked, moved his eyes, or in general was distracted from the stimulus in any way).

Procedure

In all cases the subject was dark-adapted for 30 min, and subsequently adapted for 5 min to the background luminance. The 50% detection threshold of the modulation was determined by means of a modified method of constant stimuli, as follows.

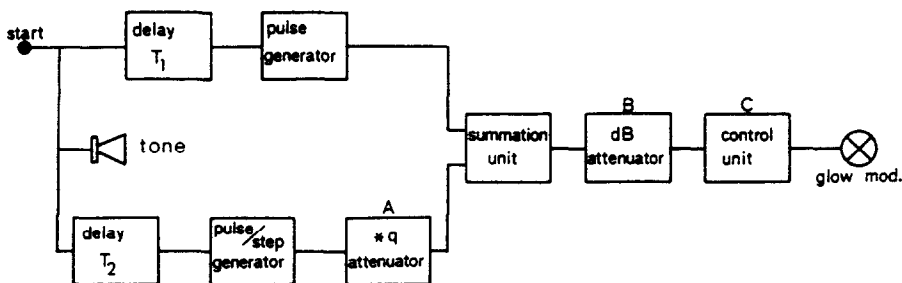


Fig. 6. Block diagram of the circuitry applying the perturbation technique. The variable is $T_2 - T_1$ while the attenuation of A is such that the ratio of test and probe stimulus equals q . Attenuator B controls the amplitude of the combination. Unit C controls and linearizes the glow modulator.

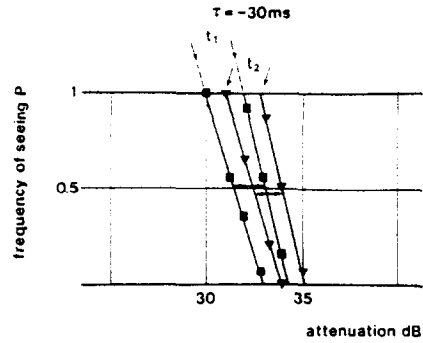


Fig. 7. Examples of two pairs of psychometric functions associated with two identical stimulus pairs measured at different times t_i (impulse response, U_s^* , $q = 0.15$, $\tau = 30$ msec, $E = 1200$ td). The squares are measured at t_1 , the triangles at t_2 .

For a certain modulation amplitude, 10 or 20 identical stimuli (depending on the experiment) were presented successively and the detected percentage was determined. The dB attenuator was readjusted and the detected fraction was again determined. On average, 4 amplitudes taken in random order were needed to get sufficient data between 20% and 80% detection chance for approximating the psychometric function on a dB scale by a straight line (Roufs, 1974c).

Immediately afterwards, in order to minimize the effect of non-stationary sensitivity changes, a different stimulus to be compared with the first was presented, following an identical routine. In most cases, the measurement of a fast pair was repeated an even number of times in counterbalanced order. If more than two different stimuli were to be compared, the whole set of stimuli was first completed in random order and then repeated in the reverse order and so on. The number of trials was about 800 per 30 min. Every 30 min or so, a pause of 15 min was interposed. The subject was not informed of either the type of stimulus or of its amplitude. Other relevant details or deviations from this procedure will be given in Results.

Two of the subjects were the authors. Subject F.B. had no previous experience in psychophysical work.

He was 27 years old at the time of the experiments, has normal acuity, but was medium deuteranomalous. Subjects J.P. and J.A.J.R. were well trained and were respectively 29 and 46 yr old. Both had normal vision, J.A.J.R. having a slight correction.

RESULTS

Symmetry and repeatability of measured impulse responses; a methodological reconnaissance

In practice, the usefulness of the perturbation technique strongly depends on the precision of the thresholds. According to the expressions in Methodological concepts, differences in thresholds basically determine the shape of the resulting responses. Due to non-systematic relatively slow sensitivity drifts, to order effects within sessions (probably due to fatigue) and to sudden non-systematic sensitivity shifts and learning effects, the spread between thresholds is considerably larger than within. Consequently, threshold variance is not simply inversely proportional to the number of trials constituting the samples of the psychometric functions (Roufs, 1974a, c). To optimize precision, the sample strategy has to be chosen carefully. Important is the rapidity of measurement. Looking for an adequate design, we tried out several strategies and these will be discussed further on.

Figure 8 shows three normalized impulse responses of subject J.A.J.R., using rectangular pulses of 2 msec, superimposed on a 1200 td background. In experiment (a) the response was found by using the slope method (equations 12, 13).

q was changed in five small steps of 0.1. In this particular case the order of measurement was q {0.1; -0.1; 0.2; -0.2; 0}, implying partial counterbalancing. For every value of q a 50% threshold was determined (see Apparatus and procedure) based on about seven fractions of 10 trials. The complete sequence of

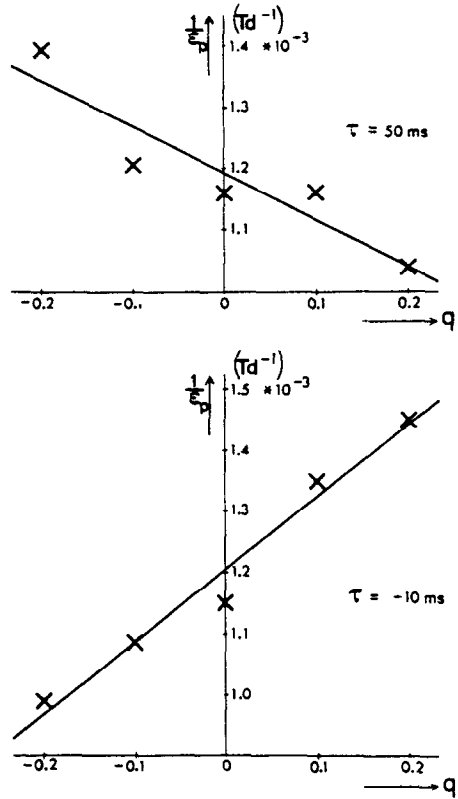


Fig. 9. Two representative examples of sensitivity $1/\epsilon_p$ as a function of the intensity ratio q . At the top the interval $\tau = -10$ msec, bottom $\tau = 50$ msec. The sign of the slope reflects the sign of U_p^* according to equation (13).

q 's was repeated twice and the three thresholds at every q were averaged. Linear regression was applied to fit a straight line through the points as a function of q (see Fig. 9). The intersection point of this line with the ϵ_p^{-1} axis provides a good estimate of the sensitivity ϵ_p^{-1} .

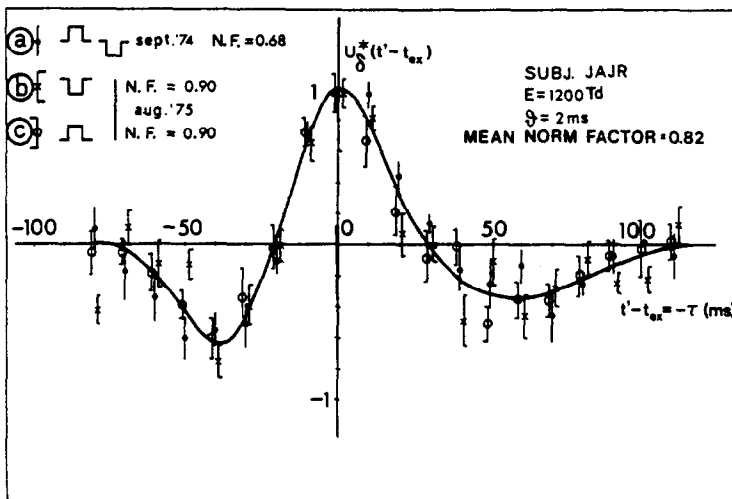


Fig. 8. Three normalized impulse responses of subject J.A.J.R., using rectangular pulses of 2 msec superimposed on a 1200 td background. Curve fitted by the eye. The vertical bars between the shrivels represent twice the SDM.

For a single 2 msec flash the norm factor $U_d(t_{ex})/a$ was found by using equation (5) and averaging over all "slopes".

The complete experiment involved 9560 trials, distributed over seven sessions. The order of measurement on the τ -axis was random, as will be the case in all the following experiments. The mean slope of the 285 psychometric functions was -0.29 dB^{-1} (cf. Fig. 7), corresponding to a Crozier quotient $\sigma/\epsilon_1 = 0.16$. Here ϵ_1 is the intensity increment of a single rectangular flash, with a detection probability of 50%. The symbol σ stands for the standard deviation of the probability density function, which is the derivative of the psychometric function (see Roufs, 1974c).

In order to check the repeatability over longer periods of time, the experiment was done again about 1 yr later. At the same time we wanted to verify whether an incremental and a decremental flash would give identical responses except for the signs, which is to be expected in the case of linear processing. Figure 8(b) and (c) show the normalized impulse responses to decremental and incremental flashes respectively, of which the negative and positive norm factors are given in the legend. (As the probe flash was always incremental, the subject detected an incremental flash in all cases.) Note that the different periods of measurement result in different average norm factors. The points were calculated with equation (18). In order to suppress the effect of sensitivity drift as much as we could and at the same time measure responses to decremental and incremental flashes in consecutive pairs, a very fast method was used in this case.

In experiments 8(b) and 8(c) we used only two q -values, $q\{-0.3; 0\}$ and $q\{0.3; 0\}$, respectively. Moreover, at every q -value only one perceived fraction of

20 trials was used to determine the 50% threshold, provided this fraction was between 20% and 80%. This was done by using a constant slope, based on an a priori Crozier quotient of 0.19 of subject J.A.J.R., arrived at from an average of many earlier measurements. Starting with $q = 0.3$ and $q = 0$, we took $q = -0.3$ and $q = 0$ immediately afterwards. To increase precision, this was repeated nine times and the pair differences were averaged. Experiments (b) and (c) each took 8000 trials during nine sessions.

Figure 8 shows that: (a) the results are repeatable within experimental error, and (b) the shape of the responses of increments and decrements in normalized form is not significantly different.

This supports the linearity hypothesis. It has to be kept in mind that, as said before, we do not know which of the responses (b) or (c) has a positive extreme value. Anyhow, the sign of the extremum of (b) is opposite to that in (c). In order to predict thresholds of any type of fast modulation, a continuous response function is wanted and also a normalization factor has to be known. To this end, a continuous curve was fitted by eye through all experimental points of Fig. 8. The overall averaged norm factor is the mean of the absolute value of the three separate norm factors. The typical shape, of the response, the total time integral being about zero, supports the hypotheses of the band-pass filter processing for this stimulus condition (1° , dark surround).

The large number of thresholds of identical stimuli measured during one session provides statistical information of systematic threshold drift during one session.

Figure 10 shows 50% thresholds ($q = 0$) obtained during experiments (b) and (c). A systematic increase of threshold is clear over a prolonged period of

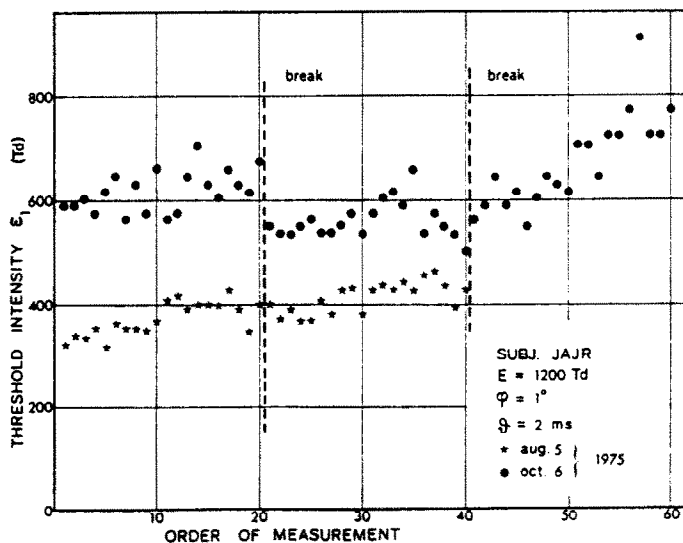


Fig. 10. The 50% threshold of single rectangular flashes of 2 msec plotted against the order of measurement for two days. The result shows relatively large interthreshold spread superimposed on a systematic order effect. Note the partial recovery after the breaks and the excessive order effect when the subject becomes exhausted. Note also the relatively large difference between the two extreme days.

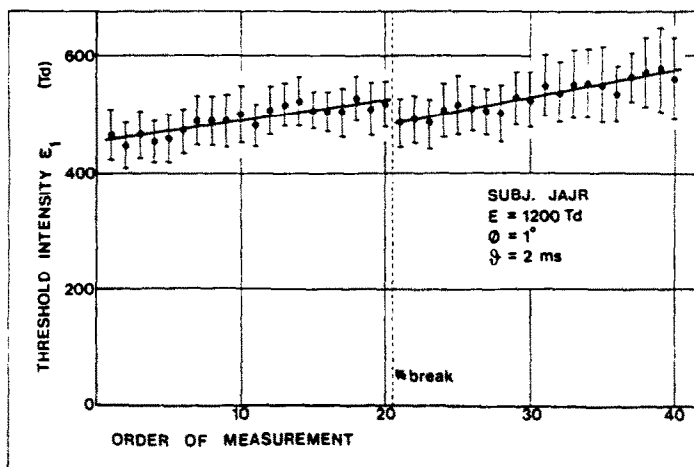


Fig. 11. Mean thresholds of single rectangular 2 msec flashes, averaged over nine sessions, plotted against number of measuring order. The intervals between the two shrivels equal two SDM.

measurement. The relatively strong increase during an (exceptional) third session suggests fatigue as a probable cause.

Figure 10 also shows by way of example how large the differences between two days can be in extreme cases.

In Fig. 11 thresholds of 9 sessions are averaged over each number of order. The small spread in the standard deviation of the means again reflects the overruling effect of interday variability in this case. The straight lines, obtained by linear regression, have slopes of 2.2 td/min and 2.9 td/min respectively.

Relation between impulse and step response to a 1° field

An effective test of linearity can be found in the relation between step response and impulse response (the latter ought to be the derivative of the former).

In actual experiment, peak detection and linearity are in fact tested in combination. Figure 12(a) shows an impulse response of subject F.B. obtained with a rectangular test flash of 2 msec at a 1200 td background. The response was calculated with equation (18) from two thresholds, q being 0.15 and -0.15 . The calculated values were averaged over five pairs, measured in counterbalance and involving ten psychometric functions each having about four fractions of twenty trials. Per session two or three different points on the τ -axis were measured. The whole experiment took 21,140 trials.

Figure 12(b) shows the step response obtained for subject F.B. under identical conditions. Due to the much smaller threshold for a step, the q -values used here were 0.02 and -0.02 . In this case all pairs on the τ -axis were measured in one session and averaged afterwards over five sessions. To complete the experiment, 14,280 trials were needed. The dashed curves are the results of a simultaneous computer fitting of both pulse and step results, under the condition that the impulse response is the derivative of the step response.

The fair fit of the curves shows that within experimental error this condition is satisfied. The norm factors are calculated as before.

For this subject, too, order effects were found, comparable with those shown in Fig. 11. In addition the averages of the single-flash thresholds within sessions reflect some effect of training (see Fig. 13).

In Fig. 14 the effect of the technique is demonstrated in graphs. For graph A only positive q -values are used, while for B, negative ones are used to calculate the response, as described in the legend. For graphs C and D consecutive pairs are used. The improvement is evident. In order to investigate the suitability of the sample strategy used, Table 1 compares the predicted spread with the experimental findings. In row 1 the standard deviation of the mean of five values of the measured $U_j(t_j)$ averaged over all j 's is shown. The data in the second row are calculated from the *a priori* SD's of the thresholds, applying Gaussian error propagation to formula (18). The *a priori* SD's of the 50% thresholds are calculated with:

$$s(\epsilon_p) = \frac{\sigma}{\sqrt{N \sum W_j}} \quad (19)$$

Here N is the number of trials per sample, W_j are the Müller-Urbán weighting functions and σ is the SD of the probability density function derived from the slope of the psychometric functions at the 50% point (Roufs, 1974c). To estimate these values we take the average slope of the psychometric functions and the average number of samples having fractions between 20% and 80% in the experiments. The actual experimental data and the predicted values are very close.

Since statistical data of the norm factors obtained by the individual pairs are available, the spread in results if no references were used can be calculated. The effect is demonstrated for singlets in row 3 if only measurements stemming from one session are used, in row 4 if the data stem from different sessions.

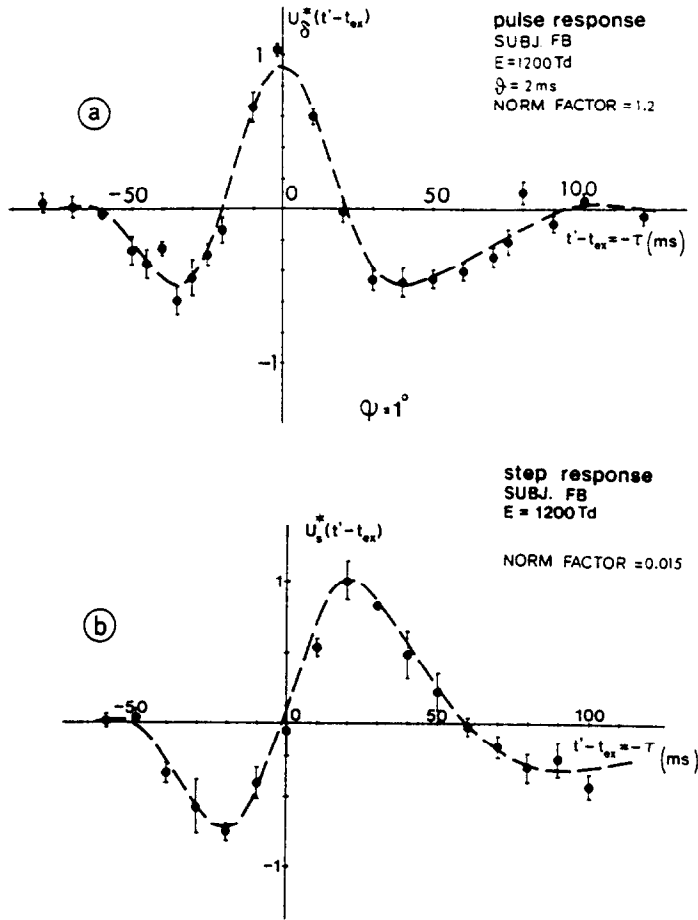


Fig. 12. Figure (a) shows the normalized impulse response. The dots are the mean values obtained after reduction by dividing the response by its extreme value. This value is given in the legend as norm factor. Figure (b) is the normalized step response. The dashed curves are the results of a simultaneous fitting, the pulse response being the exact derivative of the step response. As a result of the fitting procedure, the extreme value of the pulse response curve does not quite equal 1.

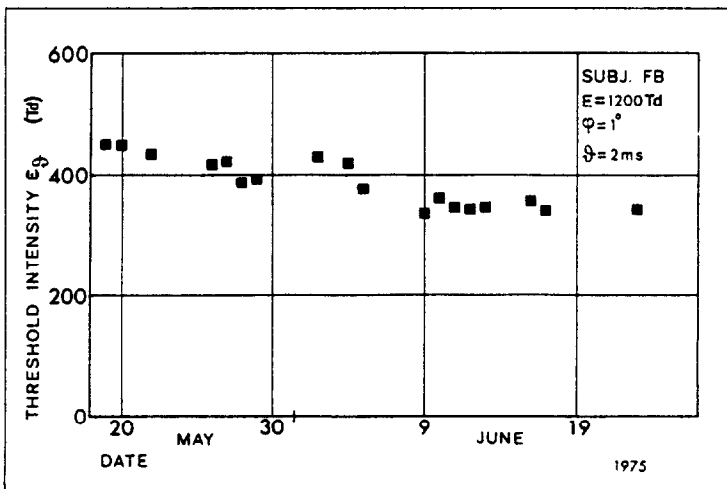


Fig. 13. Daily averages of 12-13, 50% thresholds of single rectangular 2 msec flashes derived from pairs according to equation (17) and plotted against the date for subject F.B., showing a training effect.

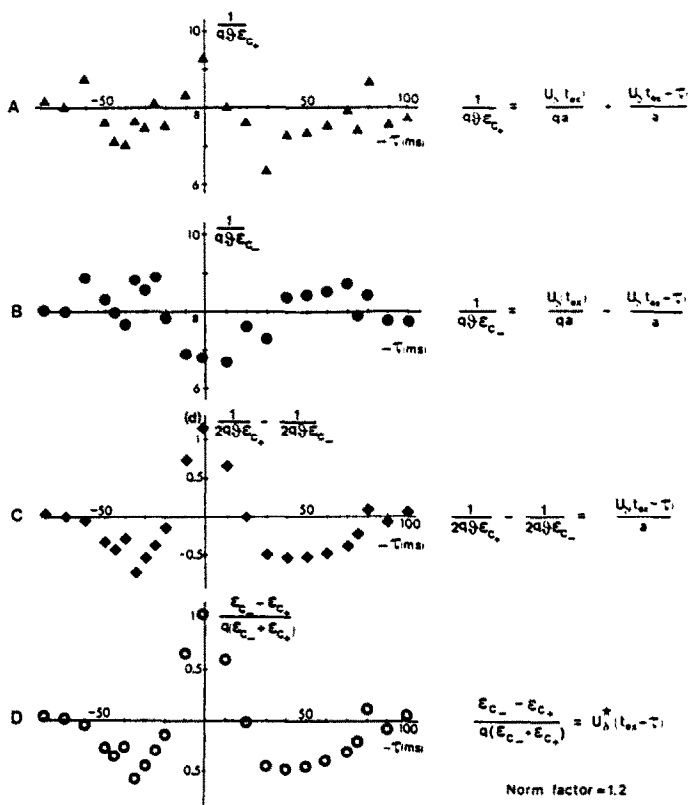


Fig. 14. Four steps to demonstrate the effect of a reference on the accuracy of the measured pulse response. The graphs A and B are the average responses to incremental and decremental flashes calculated with equation (8), taking negative q 's for the decremental flash. Graph C shows the impulse response calculated from consecutive pairs and using equation (17). Finally, graph D shows the normalized response and the average norm factor. This response is used in Fig. 12(a).

Table 1.

Standard deviation of	Pulse response $U_1^*(t_j)$	Step response $U_1^*(t_j)$
Results from the experimentally determined threshold pairs	0.07	0.10
Results from the threshold pairs, calculated a priori from the experimental slope of the psychometric function with equation (19)	0.06 (based on an average within-thresholds value of $\frac{s(\epsilon_1)}{\epsilon_1} = 0.03$, stemming from the slopes)	0.09 (based on an average within-thresholds value of $\frac{s(\epsilon_1)}{\epsilon_1} = 0.03$, stemming from the slopes)
Results from the experimental single thresholds at identical flash intervals measured scattered within sessions*	0.18 (The value between thresholds within-sessions is $\frac{s(\epsilon_1)}{\epsilon_1} = 0.08$)	0.21 (The value between thresholds within-sessions is $\frac{s(\epsilon_1)}{\epsilon_1} = 0.07$)
Results calculated from measured threshold spread of singlets scattered all over the sessions	0.24 (The value between sessions is $\frac{s(\epsilon_1)}{\epsilon_1} = 0.08$)	0.22 (The value between sessions is $\frac{s(\epsilon_1)}{\epsilon_1} = 0.02$)

* The number of trials for a singlet is equal to the total number of trials used for a pair.

Perceptual phenomena in connection with 1° fields

In all the cases so far, the detection criterion was a typical change in the visual field, termed "agitation" and not an increment in brightness.

Band-pass filter processing and De Lange characteristics

In Fig. 15(a) and (b) the gain curves of the subjects are shown as dashed lines. These are found by taking the modulus of the Fourier transforms of the impulse responses of Figs 12(a) and (8) respectively.

The predicted gain curves have a band-pass filter character. This supports an earlier suggestion that for relatively large stimuli the perceptual attribute "agitation" which accompanies transients is linked with a separate variable (Roufs, 1974a). The fine and widely dotted lines in Fig. 13(b), belonging to the D and C filters taken from that article and Roufs (1974c), are calculations of the gain of this variable based on entirely different measurements. The C-type filter especially looks rather close. For comparison the De Lange flicker fusion curves are shown for the same subject and for the same stimuli, although measured quite some time earlier. The experimental amplitude sensitivities are the reciprocals of the 50% thresholds, obtained from psychometric functions of gated sinusoids. Subject J.A.J.R. terminated each trial himself and therefore the number of peaks was determined by his decision time, whereas subject FB was presented

with exactly 15 fully fledged peaks in order to favour the same "probability summation" effect for all frequencies.

This limits the frequency range at high values since the time that the gate is open becomes too short with respect to its slopes. The experimental amplitude sensitivity curve as a whole is situated about 0.25 log units upwards with respect to the one calculated from the impulse response, which is caused by "probability summation", and is consistent with the estimate based on the known Crozier quotient for single flashes (Roufs, 1974c). On top of that the flicker fusion curves at low frequencies tend to a horizontal asymptote, whereas the gain derived from the impulse response is almost zero at these frequencies. This supports the idea of the two channels, as explained in the introduction and illustrated in Fig. 1, the frequency content of an impulse being mainly transferred in the high-frequency band-pass channel.

The effect of background luminance

Apart from a scale factor, the threshold curves of rectangular flashes over a long duration range are identical in shape at highly different background levels (Roufs, 1974a). The model suggests that this could be due to the similarity in shape of the impulse responses at these levels, except for a change in time scale (Roufs, 1974a, Fig. 9). In principle this can now be verified. To that end a impulse response of the 1° stimulus was measured superimposed on a 2 td adap-

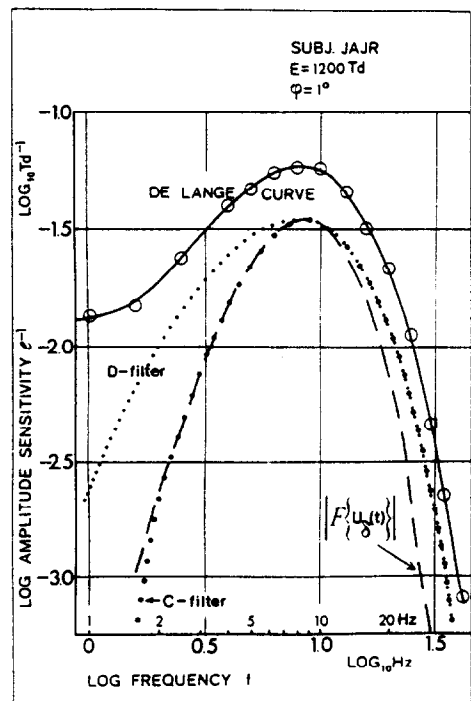
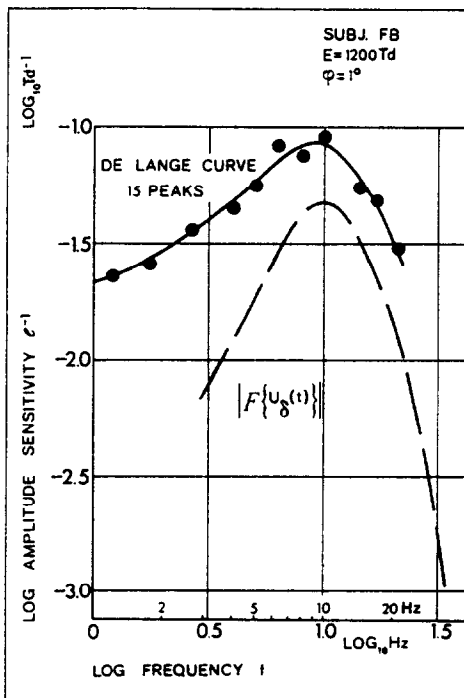


Fig. 15. The absolute value of the Fourier transforms of the unit impulse response of two subjects are shown as a function of frequency (dashed lines). For comparison, measured amplitude sensitivities are plotted (continuous lines). For details, see text.

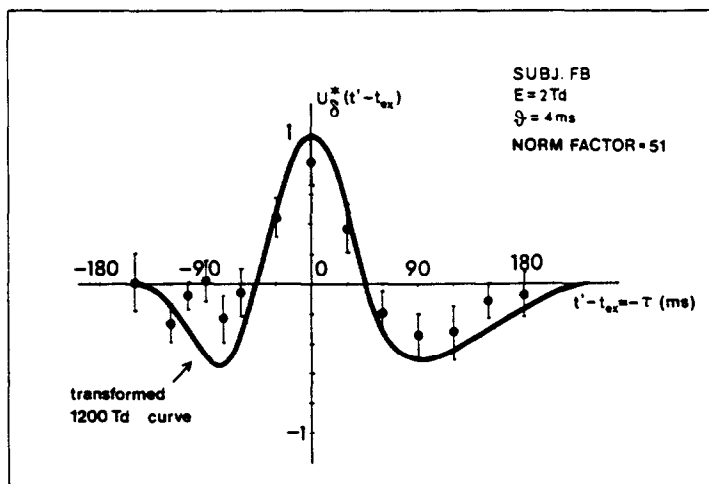


Fig. 16. Dots represent the experimentally obtained impulse response on a 2 td background level at various time intervals τ between probe and test stimulus onset. Bars indicate the SDM. The drawn line is the impulse response obtained at a 1200 td level, its time-unit being multiplied by a factor 2.5.

tation level. This was the lowest level suited for reasonable measurement and consequently yielded the slowest obtainable response. Unfortunately, in the course of the measurements it became clear that we had taken the level a bit too low, since the subject found his measurements hampered by frequent fading of the image due to Troxler's effect, by irregularly appearing clouds of "Eigenlicht" and other disturbing effects which usually accompany low level measurement. The measurements were experienced as very tiring. Probably as a result of all this, the spread was found to be considerably higher than at the 1200 td level. Yet, it seems worthwhile to compare the results. Figure 16 shows the measured impulse response at the 2 td level.

It was obtained by the pair method taking 15,300 trials. From these trials 196 psychometric functions were obtained, giving rise to 98 threshold pairs of which seven response data were averaged for any of the fourteen values of τ . In order to facilitate comparison, the normalized impulse response obtained for the same subject at the 1200 td level is shown (solid line), the time unit being scaled up by a factor of 2.5.

Given the very large difference in luminance, there is indeed correspondence between these low level measurements and the data obtained in the previous section.

Impulse and step response of a point source

Impulse and step responses do not change much with background level, except for the time scale, if the stimulus dimensions are sufficiently large and the background is not too low. However, very small stimuli show differently shaped responses, which are more of the sustained type. The perceptual attributes to be detected also change.

To demonstrate this, the results for a foveal point

source are given in this section. The stimulus dia was 0.8', situated in the middle of four small and weak red fixation lights, positioned at the corners of a square having 25' sides and superimposed on a 1200 td 11° background, acting also as surround. The experimental techniques, the procedures and the theoretical assumptions were the same as in the foregoing sections.

In the case of the impulse response twelve values of τ were used. The results are averages of eight (50%) threshold pairs taking on the average 60 trials per psychometric function, amounting to 11,520 trials in total. From the 192 psychometric functions the average Crozier quotient σ/ϵ was 0.14.

In the case of the step response eleven values of τ were taken, each result being the average of eight threshold pairs, 10,560 trials being taken in total. From the 176 psychometric functions an average of $\sigma/\epsilon = 0.16$ was found.

The measured values of the impulse and step responses are given in Fig. 17(a) and (b). The dashed curves are simultaneous computer fittings of which the impulse response is the exact derivative of the step response. The time scale is somewhat extended with respect to the responses in Fig. 12, which was to be expected since, for instance, the critical duration increases if the diameter decreases (Roufs and Meulenbrugge, 1967; Adler, 1970). The monophasic responses are of the sustained type, typical of low-pass filter action. The system can be described fairly well in terms of a fourth order real pole. The normalized impulse response is

$$U_{\delta}^*(t) = 0.742 \left(\frac{t}{12.66} \right)^3 \exp \left(- \frac{t}{12.66} \right); t \text{ in msec.}$$

$$t_{ex} = 37 \text{ msec.}$$

(20)

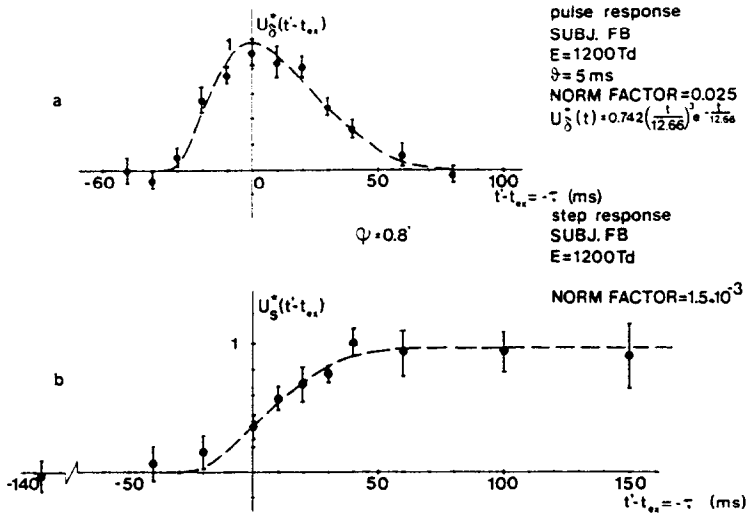


Fig. 17. Pulse and step response of a point source on an extended background of 1200 td. The vertical bars between the shrivels represent twice the SDM. The dashed curves are the results of a simultaneous fitting, the curve of Fig. a being the derivative of that of Fig. b.

The absolute value of the Fourier transform, being the gain curve of the system, is given in Fig. 18. The difference from the gain curve of a 1° field is obvious, as can be seen by comparing with Fig. 15a.

Perceptual phenomena with the point source

The perceptual attribute to be detected was either a brief or a steplike brightness increment, looking

homogeneous in space over the small stimulus. This attribute is comparable with the periodic brightness variations ("swell") in the case of low-frequency sinusoidal stimulation with 1° fields. In this case, the positive response peaks can without any doubt be attributed to brightness increments.

DISCUSSION

Evaluation of procedures

The results of the first of the procedures used, the "slope" method described in Results, encouraged the approach. No significant deviations from linear regression were found over the range of the q -values used. The relative amplitudes of the phases of the determined impulse responses in fact suggest that q -values as large as 0.3 would have been allowed, leading to a larger effect and hence to improved experimental precision. The varying slopes of the regression lines, changing with the flash interval τ , and their relatively small standard deviation gave confidence in the method. However, a set of five concatenated thresholds still takes so long that, in spite of time efficiency of the procedure, the chance of the results being obscured by sensitivity drifts was still thought not to be negligible. This led to the method of "pairs", allowing very fast measurement of concatenating pairs, although about the same experimental effort is needed to reduce the standard deviation of the averages to the desired level. From the results no clear evidence was found that this procedure is superior for the elimination of drift effects. However, the use of only two q -values proved to simplify the experimenters' task considerably. It is not essential to choose q -values that are symmetrical around $q = 0$, but it has the advantage of giving relatively large "pair differences" without introducing unsafe q -values.

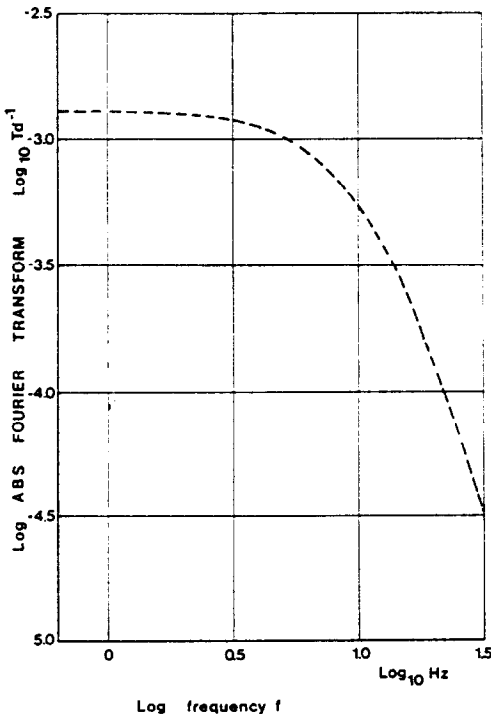


Fig. 18. Gain curve of the transfer of a point source, obtained by taking the modulus of the Fourier transform of the impulse response of Fig. 17a.

The results of Fig. 14 and Table 1 show that the obscuring effects of drift are virtually eliminated by the use of such a reference. Although the resulting precision and the repeatability over a long period of time are quite satisfactory, the actual design of the experiments is rather laborious. Since about 700 trials were used for every point of the response curve, taking about 30 min in all. It needs some economizing. The present set-up gave refined information on the sources of variance, especially about the systematic drift, which we did not notice before (Roufs, 1972a).

The information given in this article may lead to a more economic design.

A more fundamental type of potential error could have been the width of the dominant phase of the probe flash, the "probing needle" being too blunt. However, this is obviously not the case.

It can be shown by rough calculations that in the actual cases the "bluntness error" is negligible in relation to the experimental inaccuracy.

Validity of concepts

The detection model is supported by several experimental results: no significant deviation from the linear relation between ϵ_p^{-1} and q , according to equation (11), was found.

Neither was there any asymmetry when incremental and decremental flashes were used. The strongest support, however, is found in the correspondence between the impulse response and the derivative of the step response as shown in Figs 12 and 17.

This implies that the threshold of any time function should be predictable by calculating its unit response by convolution and determining the reciprocal of its extreme value (equations 2 and 6). This appears to be the case in all cases we have investigated, as will be shown in a subsequent paper. In the case of stimuli that are considerably larger than point sources, precautions have to be taken to ensure that the function changes sufficiently fast, otherwise we get a mix-up of the two systems referred to in the introduction.

If the sign of the extreme value of a response is opposite to that of the dominant phase of the probe response, the ratio of d^+ and d^- has to be tested by measuring the threshold of a short incremental flash in relation to a decremental one and making use of equation (5). (This is for instance the case for an incremental rectangular flash of a certain duration, as will be demonstrated in the related article.) In the case of the foveal 1° field this ratio was shown to be 1 (Roufs, 1974a).

In the literature several other models concerning the prediction of thresholds on the basis of systems analysis can be found. In comparing their performance we shall restrict ourselves to the most closely related work. Kelly and Savoie (1978) derived impulse and step responses from a postulated transfer function, the modulus of which was fitted to flicker fusion data, ignoring the difference in perceptual attributes at low and high frequencies. Their model is a linear

filter followed by an asymmetric rectifier, which is effectively the same as ours, d^+ and d^- having different values under their conditions and from their point of view. They compared threshold ratios of an incremental flash of an 8° uniform field and of a temporal rectangular modulation of an 8° , 4c/deg grating, both as a function of duration. From their calculated responses they concluded that the system is much more sensitive to negative than to positive response phases. However, neither Rashbass (1970) with a 17° field nor Herrick (1956) or Roufs (1974a) with a 1° field at comparable background levels found any significant asymmetry. As pointed out before (Roufs, 1974a, p. 836) asymmetry may be found and is even likely under certain conditions. Rashbass (1970; 1976) proposed an interesting model to predict thresholds from luminance changes, of which the essentials are also used by Broekhuijsen *et al.* (1976) and Watson and Nachmias (1977). In his view, a signal proportional to the luminance change passes successively a linear (band-pass) filter, a quadratic operator and an ideal integrator, operating over a time T which is large with respect to the duration of the signal. The luminance change is thought to be detected if the output of the integrator surpasses a certain level. As pointed out before (Roufs, 1974a), this extra integrator is the essential difference between the models since a symmetric nonlinearity without integrator does not change the results. What would our experimental results mean in the Rashbass model?

In Appendix A it is shown that our data of the 1° field are not quite as expected from his model, although the deviations are not dramatic. The point source results, however, deviate considerably, but this is to be expected if one accepts our step response, since it does not vanish for large times (which is required if the Rashbass model is used). Hallett (1969a) determined impulse and step responses of the rod system. His model is almost identical with ours, but his detection criterion and consequently his technique is quite different. Detection is based on a relation between the signal amplitude threshold a at the output of the linear filter and the background level in order to obtain a detectable signal-to-noise ratio, assuming that all noise at the output is filtered quantum noise caused by the background. He increased the level of his 18° background impulsewise or stepwise in time and measured the discrimination threshold of a small ($12'$) short flash in its centre as a function of the relative time shift of test flash and background.

Hallett pointed out that non-stationary threshold variations prevented precise determination of the response (see also Hallett, 1969b). This might be overcome by using a reference as was done in the present work. Hallett found no satisfactory relation between impulse and step response. It is not clear whether this is due to the insufficient precision of his measurements or to the properties of the detection stage in his model.

Masking with a flashed background has been used in the fovea even earlier (e.g. Crawford, 1947; Boynton and Kandel, 1957; Sperling, 1965). Application of Hallett's model to the fovea is hampered by the consideration that, especially at the relevant levels, there is no square-root relation between intensity and threshold, indicating that photon noise is not a likely candidate as a noise source at the output of the linear filter. This is also unlikely on the basis of the shifts of the amplitude sensitivity curves of flicker experiments found as a function of the background intensity (Rud-dock, 1969).

On the contrary, the constancy of the ratio of the standard deviation of the density function associated with the psychometric curves and the 50% threshold itself over about 5 decades strongly suggest that this noise is independent of background luminance (Roufs, 1974c). Ikeda (1965) and Uetsuki and Ikeda (1970) used subthreshold summation based, although not explicitly, on the same assumptions. Their responses look similar to ours, apart from small details which might be caused by the fact that in their method the test response is not always small with respect to the probe response, so that different phase combinations may determine threshold. Tolhurst (1975) also used subthreshold summation of gratings as a tool to separate the responses of the transient and sustained system. Norman and Gallistel (1977) looking for the impulse response as a basic function assumed the same systems properties. However, since they did not use the possibility of perturbation they had to postulate an extra set of properties about the shape of this function.

The nature of transfer

The band-pass character of the transfer of the output variable giving rise to "agitation" in the case of a 1° stimulus with a dark surround is confirmed. As a consequence the impulse response has a multiphasic character.

Comparing the modulus of the Fourier transform of the impulse response function with de Lange

curves, shifted downwards 0.25 logunits for reasons mentioned in Results, the gain at low frequencies is still significantly less than the de Lange curves would suggest. This gain curve can also be measured directly, using the same technique with sinusoidal perturbation frequencies (Roufs and Pellegrino Van Stuyvenberg, 1976).

The results show also a definite band-pass character as will be shown in detail in a subsequent paper. For small stimulus diameters this transient activity, described as the band-pass filter action, disappears as does the "agitation" percept. At low background levels on the other hand, it does not vanish so readily as the shape of the De Lange curves would indicate (Roufs, 1972a). This difference between small and large stimuli suggests that the band-pass filter action which accompanies "agitation" has to do with lateral interaction. Psychophysical evidence for sustained and transient activity in the human visual system was found, for instance by Tolhurst (1975), Kulikowski and Tolhurst (1973), Johnson and Enoch (1978) and Philips and Singer (1974). Implications were analysed by Breitmeyer and Ganz (1976). There is of course overwhelming physiological evidence for sustained and transient activity in the retina and more central locations (Breitmeyer and Ganz, 1976).

Also the type of sustained transfer we found for the point source (four RC networks in cascade) is known physiologically, for instance for the rod receptor of the bullfrog (Toyoda and Coles, 1975). Likewise, there is physiological evidence that lateral interaction in the case of larger stimuli results in more transient-like responses (Detwiler *et al.*, 1978). However, we prefer not to take arguments of this kind into consideration because we find it premature and philosophically not quite correct to make detailed connections between physiological evidence and psychophysical data.

In finding new support for two output variables connected with threshold perception of time-dependent stimuli, the problem of their interrelation comes up. This has still to be investigated, especially in view of suprathreshold brightness variations accompanied by induced spatial inhomogeneities.

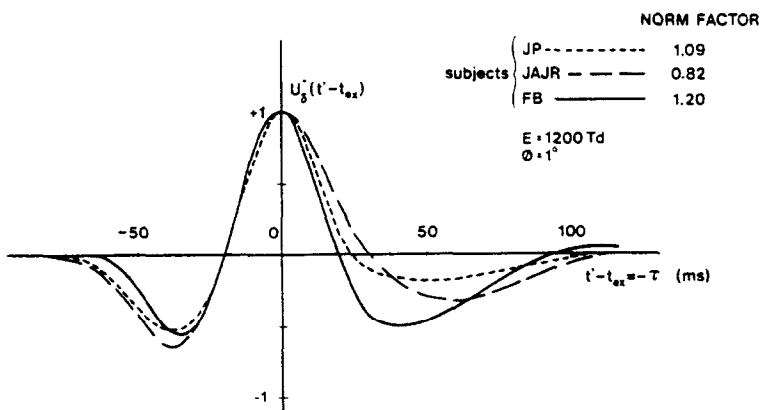


Fig. 19. Comparison of normalized unit impulse responses of three subjects.

Individual differences

Figure 19 allows intersubject comparison. The curves are essentially the same. Subjects F.B. and J.P. have a higher sensitivity (see norm factors) and smaller time constants reflected by the duration of the individual phases. Presumably this is due to age differences (see Apparatus and procedure).

In the literature it is not common to make any separate allowance for the effect of age on time constants and sensitivity. The response properties shown here result, as pointed out earlier (e.g. Roufs, 1974b), in an increase in reaction time and a decrease in critical flicker fusion frequency for older subjects. This is a common finding in literature (e.g. Weale, 1963).

CONCLUSIONS

Internal responses of one-shot functions can be determined by means of a drift-correcting perturbation technique with sufficient accuracy to allow quantitative analysis.

The results of impulse and step responses are consistent with quasi-linear processing of weak signals and peak detection. This implies that the threshold of any sufficiently fast transient should be predictable. (This will be confirmed for the tests in the related paper.)

The shape of the impulse response does not change essentially with the Plateau level, but the time scale does. On the other hand if the stimulus dimensions become very small the shape changes essentially.

For 1° foveal stimuli with dark surround the system processes one-shot stimuli as a band-pass filter. The responses are of a transient type. For an 0.8' point source on a large homogeneous background the processing is purely low-pass filtering, giving rise to sustained responses.

Between subjects only minor differences are found.

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expressed in the threshold of a single flash as a unit. The threshold intensities (A, B) of a pair are given by

$$\int_0^T [A\phi(t) + B\phi(t - \tau)]^2 dt = 1 \quad (A2)$$

which leads to the equation of an ellipse:

$$A^2 + B^2 + 2ABL(\tau) = 1 \quad (A3)$$

with

$$L(\tau) = \int_0^T \phi(t)\phi(t - \tau) dt.$$

After differentiating with respect to B :

$$2A \frac{dA}{dB} + 2B + 2L(\tau) \left\{ A + B \frac{dA}{dB} \right\} = 0. \quad (A4)$$

Since in our experiment one flash is always small compared to the other, we look at the neighbourhood $(A, B) = (1, 0)$. Equation (A4) becomes:

$$\left(\frac{dA}{dB} \right)_{1,0} = -L(\tau). \quad (A5)$$

In our language the threshold condition for the combination is:

$$\frac{\epsilon_A \theta U_{\delta}(t_{ex})}{a} + \frac{\epsilon_B \theta U_{\delta}(t_{ex} - \tau)}{a} = 1, \quad \epsilon_A \gg \epsilon_B \quad (A6)$$

Expressing the threshold intensities also in the threshold ϵ_0 of one of the flashes alone: $\epsilon_A/\epsilon_0 = A$; $\epsilon_B/\epsilon_0 = B$, and using equation (5) we obtain:

$$A + BU_{\delta}^*(t_{ex} - \tau) = 1. \quad (A7)$$

APPENDIX A1

In Rashbass's language the response $\phi(t)$ of his linear filter to a short rectangular flash at threshold is defined by

$$\int_0^T \phi^2(t) dt = 1. \quad (A1)$$

The intensities of two combined flashes at threshold, having equal durations and an interval τ , can be

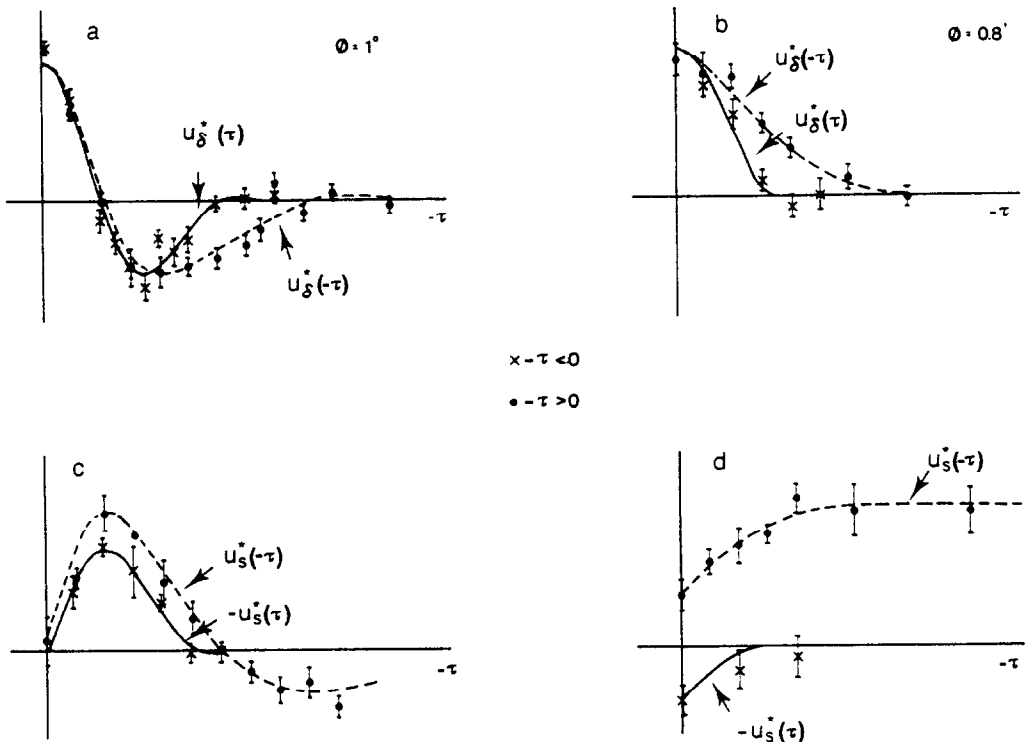


Fig. 20. Plots (a) and (b) demonstrate the degree of symmetry of the impulse responses around $\tau = 0$, at a 1200 td background for a 1° and a 0.8° stimulus. Plots (c) and (d) demonstrate the degree of asymmetry of the step response under the same conditions.

Now, for any set of experimental pairs (A, B) in particular $(A, B) = (1, 0)$ we obtain:

$$\left(\frac{dA}{dB}\right)_{1,0} = -U_s^*(t_{ex} - \tau). \quad (A8)$$

APPENDIX A2

Comparing equation (A8) with equation (A5) we see that the impulse response U_s^* obtained from our material on the basis of our model is equivalent to the autocorrelation function $L(\tau)$ on the basis of Rashbass's model. An autocorrelation function is essentially symmetric:

$$L(\tau) = L(-\tau). \quad (A9)$$

However, our experimental data do not seem to fulfil this requirement too well, as Figs 20a and b show. On the other hand, the responses of the combination predicted by the present model lead to threshold pairs which mimic rather well the ellipses predicted by equation (A3) as seen in Fig. 21.

The shapes of these curves were basic to Rashbass's model. A combination of a short flash and a step

expressed in their respective thresholds has in Rashbass's model the threshold criterion:

$$\int_0^T [C\phi_s(t) + D\phi_s(t - \tau)]^2 dt = 1. \quad (A10)$$

After some elaboration one obtains:

$$\begin{aligned} \left(\frac{dC}{dD}\right)_{1,0} &= -\int_0^T \phi_s(t)\phi_s(t - \tau) dt \\ &= \int_0^{-T} \phi_s(t)\phi_s(t - \tau) dt \end{aligned} \quad (A11)$$

$\phi_s(t)$ being the unit step response of the linear filter.

In our model the threshold criterion for the combination of an impulse and step is:

$$\frac{\epsilon_C \theta U_s(t_{ex})}{a} + \frac{\epsilon_D U_s(t_{ex} - \tau)}{a} = 1. \quad (A12)$$

Using again the thresholds ϵ_{C0} and ϵ_{D0} of impulse and step as intensity units, one obtains:

$$\frac{\epsilon_C}{\epsilon_{C0}} + \frac{\epsilon_D}{\epsilon_{D0}} U_s^*(t_{ex} - \tau) = 1 \quad (A13)$$

or

$$C + DU_s^*(t_{ex} - \tau) = 1 \quad (A14)$$

and from this:

$$\left(\frac{dC}{dD}\right)_{1,0} = -U_s^*(t_{ex} - \tau). \quad (A15)$$

APPENDIX A3

The autocorrelation function of the step response, referred to as L_s by Rashbass is:

$$L_s = \int_0^T \phi_s(t)\phi_s(t - \tau) dt. \quad (A16)$$

Combining equation (A16) with equation (A11) and (A15) one obtains:

$$\left(\frac{dC}{dD}\right)_{1,0} = -\frac{d}{d\tau} L_s = -U_s^*(t_{ex} - \tau). \quad (A17)$$

and since $L_s(\tau) \equiv L_s(-\tau)$:

$$\left(\frac{d}{d\tau} L_s\right)_\tau = -\left(\frac{d}{d\tau} L_s\right)_{-\tau}. \quad (A18)$$

In our language:

$$U_s^*(t_{ex} - \tau) = -U_s(t_{ex} + \tau).$$

This means that our step responses should be anti-symmetric around t_{ex} , as defined for the pulse response, according to Rashbass's model. Figure 20 shows that the experimental values deviate considerably from this behaviour, especially for the point source.

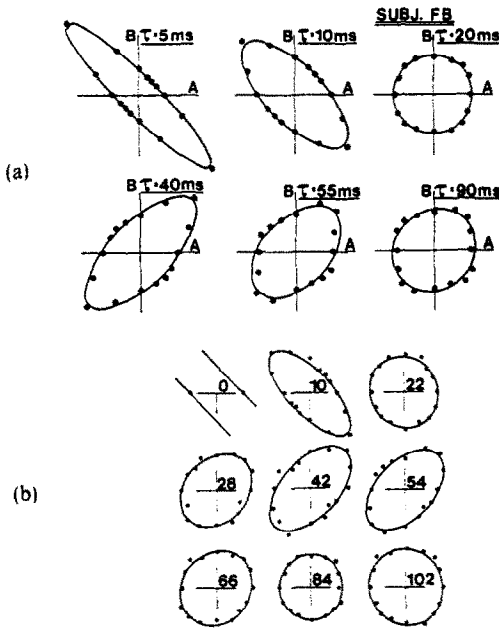


Fig. 21. Plot (a) shows thresholds of flash combinations of incremental and decremental flashes predicted by equation A6 on the basis of the experimentally determined unit impulse response. The ellipses are least square fittings. Plot (b), a copy of Rashbass's Fig. 4 (1970) is given for comparison. His experimental points were obtained according to equation (A3), through which he fitted the ellipses shown.