Discrimination of visually perceived intervals of time

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The discrimination of short intervals of time, demarcated by a foveally presented spatially distinct double pulse of light, was studied under several conditions of pulse intensity, angular diameter, and duration. We defined temporal acuity as a measure of discrimination capacity in terms of d' values. It is shown that the acuity mechanism uses largely integrated information—in the spatial and temporal domain, up to at least 56' and 32 msec, respectively. Acuity increases slightly with increasing integrated pulse energy, but seems quite independent of the presence of an adapting field of appreciable brightness. Studies on the effect of the foveal site aimed at by the pulses of light have shown that temporal projections lead to significantly poorer acuity values than nasal projections. Monoptic and dichoptic stimulation, however, are fully equivalent.

If two short pulses of light are presented at different moments to separate sites in the visual field, they may be perceived either simultaneously or as being more or less distinct in time. We have termed the ability to discriminate between such intervals of time "temporal acuity."

Double-pulse experiments in vision have been performed under a variety of conditions. If pulses are coincident in space (homogeneous double pulses, for a review see Boynton, 1972), brightness thresholds can be measured as a function of the temporal separation of the pulses (Rashbass, 1970). In such experiments, temporal integration phenomena can only be investigated at very low stimulus intensities. This restriction is obviated when studying the threshold for the perception of the dark interval between pulses of appreciable brightness. With central fixation, Mahneke (1958) obtained a just noticeable dark interval, for pulse durations up to 50 msec, at a stimulus onset asynchrony of about 60 msec. This is much shorter than the 230 msec Efron (1970) reported with parafoveal stimulation, asking the observer to indicate whether both flashes do or do not overlap in time. In both cases, stimuli are delivered either monoptically or dioptically. It seems likely that the mechanisms responsible for the effects observed are mainly of retinal origin, probably with the exception of Efron's findings.

A second group of experiments has been performed in the interest of apparent movement phenomena and masking effects. In this case, pulses are delivered to different retinal areas. Apparent movement is perceived

with heterogeneous double pulses under a variety of experimental conditions (see, e.g., Graham, 1965). Even if both pulses are not perceived as spatially resolved, an extended movement illusion may be evoked. Biederman-Thorson, Thorson, and Lange (1971) have used the illusion as a cue for the detection of the temporal order of spatially unresolved pulses, in the peripheral field of vision, when these were presented with a varying temporal interval. Optimal detection occurred with time intervals of 30 to 50 msec. Apparent movement perception (as well as real movement perception) seems to involve mainly central processes, as it may persist in dichoptic presentation (Biederman-Thorson et al., 1971).

Our main point of interest is the temporal accuracy of central signals generated by a pulse of light. Single-flash duration-discrimination experiments (e.g., Allan & Kristofferson, 1974b; Allan, Kristofferson, & Wiens, 1971) seem to serve this purpose very well. Indeed, they yield good discrimination for duration differences between 20 and 40 msec. Though differences in apparent brightness between different duration flashes do not seem to be used (Allan et al., 1971) in duration discrimination, effects of differences in total energy per flash are likely to complicate the interpretation of results. Most important, however, is that discrimination is based on the trailing edge of the internal flash-induced signal, whereas the leading edge of a response to light is likely to be of more importance for the determination of temporal relationships to other events. Moreover, the leading edge of a neural response, or the response to a very short pulse, is likely to be more linear, therefore more reproducible in successive presentations.

Light-tone pair duration-discrimination experiments (e.g., Allan, 1975a, 1975b; Allan & Kristofferson, 1974a) which have the advantage of not relying on

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memory for the discrimination task, certainly call for a central mechanism. However, discrimination is still based on the respective stimulus offsets.

Our approach was to study temporal accuracy by the effects of central interactions of two light-pulse-generated signals. To ensure that the leading edge of neural responses is used and a central mechanism is stimulated, we employed dichoptic stimulation by a pure time interval demarcated by a spatially resolved double pulse of light (see Figure 1). This time interval will be referred to as the stimulus, the magnitude of which is defined as the lapse of time between the onsets of the first and second pulse. The mechanism under study, which we will refer to as the temporal acuity system, was identified as a central mechanism (i.e., a postretinal mechanism) by comparing results with monoptic and dichoptic stimulations.

To gain further insight into the nature of the temporal acuity system, we studied its dependence on the energy of the pulses of light, the ranges, spatial as well as temporal, over which the system effectively integrates information, and the effect of light adaptation and the associated background field. We expected the acuity to be limited by internal noise, the amplitude of which can at least partially be manipulated by the visual inputs. Changes in acuity as a function of input characteristics might thus yield information about the noise in the neural signals representing these stimuli.

METHODS

Apparatus

Time intervals were presented dichoptically in most experiments, demarcated by the onsets of two rectangular pulses of light (cf. Figure 1). These stimuli arbitrarily were defined positive if the first pulse was the leftmost one in the visual field (not necessarily the one transmitted to the left eye). Two television projection tubes with white P36 phosphor (rise time ~ 0.2 msec, negligible afterglow) served as sources of light.

As shown in Figure 2, the pulses of light reached both eyes through separate optical paths of equal lengths. Each path contained a set of diaphragms for selecting the diameter and site of the spot, a filter holder, prisms, and a beamsplitter for directing the optical path to a viewing telescope (angular magnification 2.5) which provided fixation and fusion markings.

Figure 1. Functional diagram of the detection system. The stochastic processor, P , receives input from both eyes (dichoptically) or one eye (monoptically); this consisted of two-flash responses to pulses having a temporal separation of T_j . The output signal, $X(T_j)$, is a stochastic variable having a density function, $f(X | T_j)$, conditioned by T_j . The detector, D , tests a sample from the signal, $X(T_j)$, for exceeding predefined levels, and responds accordingly.

Figure 2. Top: Diagram of the two-channel optical system. The abbreviations are as follows: L, TV-projection tube; S, diaphragm for site and diameter of spot; F, neutral density filter; P.M., photomultiplier; dich. ↔ mon., movable components for projecting the left channel into the right eye for monoptic stimulation; B, lamp and field stop for background illumination in Maxwellian view; Obj. and Oc., frontlens and ocular lens of the viewing telescope; F.M., fixation and fusion markings in the image plane of S. Bottom: Diagram of the images as seen by the left and right eye in case of dichoptic presentation. Site of the light pulses is indicated by small circles. For dimensions see text.

These markings (see Figure 2) consisted of faintly red, illuminated diagonal cross hairs subtending about 30° from the eye. The diameter of the spot on the retina may be set in the range of 15 to $240 \mu\text{m}$ (viewing angle, $3.5'$ to $56'$). The distance of its center from the fixation point may be varied from 75 to $900 \mu\text{m}$ nasally or temporally (viewing angle, $17'$ to $3^\circ.30'$). All stimulation thus was foveal, in most cases even restricted to the center of the fovea. If not mentioned otherwise, stimulation sites used were $70'$ ($300 \mu\text{m}$) nasally, and pulse diameters were $7'$ ($30 \mu\text{m}$) for both eyes.

Pulse intensities were monitored by a photomultiplier and were set by neutral density filters in steps of 0.6 log units. Zero log intensity was set at about 5 log units above photopic (foveal) threshold with continuous light at sufficient angular diameter to be outside the range of spatial summation. Pulse durations were either 0.2 msec or in the range from 8 to 500 msec. Apart from these measures, we also used the measure of pulse energy, defined to be proportional to the total number of photons within a pulse, i.e., proportional to [inten-

sity $\times$ duration $\times$ (angular diameter)²]. To indicate the equivalent pulse brightness range the dimmest pulse was about 2.5 log units above photopic threshold.

A circular field continuously illuminated by an incandescent lamp could be reflected into the visual field of both eyes to allow the setting of different adaptation levels. Zero log intensity was arbitrarily set at approximately 2.5 log units above photopic threshold. The field was seen in Maxwellian view at angular diameters up to 24°. Both intensity and diameter of the field were varied.

Procedure

The experiments were performed according to either a yes-no or a rating instruction, without feedback. During each observation period, two pulses of light were presented with an interval of time that was randomly chosen from a set of two to five (usually four) possible values, always including the zero stimulus, i.e., simultaneous pulses. In general, the probability of occurrence for each stimulus value was the same. Following a yes-no instruction, the observer only had to indicate whether the stimulus was perceived as zero or as nonzero. This means that for this task he had to uphold only one response criterion. In case of a rating instruction, however, the observer had to respond to each presentation by indicating that stimulus value which he deemed to be the most probable one presented. Thus, he had to maintain a number of response criteria, one less than the number of stimulus values.

Technically, the random choice of one of the stimulus values was obtained by reading out an electronic shift register running at 10 μ sec per position, at a length preset to the desired number of alternatives. The readout was made $\frac{1}{2}$ sec after the observer pushed the start button for a stimulus, and it then selected the appropriate delay between the triggering of two pulse generators for each optical channel.

Observations were made in series of 250 trials, which took about 10 to 15 min, preceded by 10 min of dark adaptation and several off-line trials to fix the response criteria, after which the conditions were changed in a predefined order. Mostly, four such series were recorded for each experimental condition. With a stimulus series of four possible intervals of equal probability, this amounts to 250 trials per stimulus, on the average.

For every trial, the stimulus and the response were recorded on paper tape. The several series of 250 trials for one experimental condition were read from the tape in blocks of 50 trials, yielding a number of matrices of conditioned probabilities $P(i|j)$, i.e., the probability of finding a response R_i , given the presentation of stimulus T_j . For every element of these matrices, the mean and standard error could be calculated, thus yielding a total probability matrix as raw data for further analysis.

In the text, the standard error in the last decimal is given in parenthesis behind each value obtained; in the illustrations, this is shown as a line segment adjacent to each point.

EXPERIMENTS 1 AND 2

Since our stimulus was presented by means of two pulses of light, its perception might depend on the characteristics of those pulses, as well as on the experimental conditions under which they were presented. A number of experimental factors have been investigated to determine their effect on the ability to discriminate these stimuli. Also, it seemed worthwhile to validate a detection theoretical analysis as outlined below.

In preliminary experiments (cf. Oostenbrug, 1975), it was found that the system showed fair symmetry for positive and negative stimuli, i.e., for the second

pulse of the pair to the right or to the left of the first one in the visual field. This justifies the use of a detection curve that is symmetric as to time. All experiments described here thus were performed with positive stimuli only. Stimulation was with 0.2 msec-duration pulses, 70' nasal with 7' diam at zero log intensity.

Analysis

The mechanism. The obtained experimental data are the conditional probabilities $P(i|j)$ for the observer to respond R_i after being presented with stimulus T_j . For the analysis of these conditional probabilities, signal detection theory provides the mathematical tools, described elsewhere in detail (e.g., Green & Swets, 1966; Nachmias, 1972; Wright, 1974). Basically, a stochastic correlate, $X(T_j)$, of the physical stimulus, T_j , is postulated; this has a certain probability of exceeding a certain criterion level (see Figure 1). The conditional probabilities thus obtained may be transformed into ROC curves (Green & Swets, 1966; Nachmias, 1972). If the probability distribution of the internal signals $X(T_j)$ is taken to be Gaussian, then, on normal-normal scales, straight lines may be fitted, giving the detection index, $d'(T_j)$, and the ratio of standard deviations, $\sigma(T_j)/\sigma(0)$, of the distributions of the internal signal upon stimulation by an interval of T_j msec and the zero stimulus, respectively (Nachmias, 1972). For all rating experiments described here, ROC curves can be fitted to straight lines with a total $\chi^2 = 716$, with 702 degrees of freedom, as in nearly all experiments each leaves just 1 degree of freedom. Thus, the Gaussian property of the internal signals is established within the framework of this detection theoretical model.

Experimentally, the ROC curve of each stimulus may be represented by as many points as there are criterion levels maintained. For an arbitrary number of stimuli and criteria (and hence response categories), the ROC curve equation is given by

$$z(i|j) = \frac{\sigma(T_0)}{\sigma(T_j)} [z(i|0) + d'(T_j)] \quad (1)$$

where the criterion as a running parameter is denoted by the index, i , corresponding to the response, R_i . The normal deviate $z(i|j)$ corresponding to the conditional probability $P(i|j)$ is given by

$$z(i|j) = \frac{\bar{X}(T_j) - C_i}{\sigma(T_j)} \quad (2)$$

where C_i are the observer-controlled criterion levels discriminating between responses R_{i-1} and R_i . Thus the detection index, $d'(T_j)$, is defined as:

$$d'(T_j) = \frac{\bar{X}(T_j) - \bar{X}(T_0)}{\sigma(T_0)} \quad (3)$$

which generally is accepted as suitable index of detectability. There exist other definitions of such indices (cf. Wright, 1974) that also depend on $\sigma(T_j)$. Empirically, some of them seem to be less sensitive to day-to-day variations. In our opinion, the index defined by Equation 3 theoretically is the more convenient one, since it is a straightforward parameter in the ROC-line equation (1). All indices may, however, be transformed into one another.

Temporal acuity. For a fixed reference stimulus, T_0 , all $d'(T_j)$ according to Equation 3 represent normal deviates from the conditional distribution of $X(T_0)$. These normal deviates are proportional to the actual, but unknown, average increments of the stimulus correlates $X(T_j)$. Then, plotting $d'(T_j)$ vs. the stimulus time interval, T_j , yields a plot of the transformation $[T_j \rightarrow X(T_j)]$ that is applied to the stimulus before its arrival at the detection site, beyond the unknown constant $X(T_0)$. This transformation may be described by the power function

$$d'(T) = (A \cdot T)^R. \quad (4)$$

It will be shown that the power parameter, R , in many cases may be held constant (in the range of 1.2 to 1.7) for one observer under very different experimental conditions. Having A within parenthesis leads to the interpretation of A as the inverse value of the stimulus, resulting in a detection index d' of unity. It may be noted that A has the dimension of inverse time, whereas d' (being a ratio) is dimensionless. In the following, we will refer to the parameter A as the (temporal) acuity, assuming that it fully describes the discriminability on a single perceptive axis in any specific experimental conditions, irrespective of explicit stimulus values, and with a fixed exponent R .

Results

Experiment 1 (Observer J.K.) was intended to verify

Figure 3. Detection indices, $d'(T)$, obtained for different instructions of the observer (Experiment 1). Numbered points indicate instruction type as defined in the text. The curve is a power function according to Equation 4 fitted to the points, with the exclusion of those resulting from Instructions 2 and 6 (see text); $A = 0.029(6) \text{ msec}^{-1}$, $R = 1.47(6)$, $\chi^2 = 16(18 \text{ df})$.

Table 1
Criterion Levels vs. Instruction in Experiment 1

Instruction 1 Criterion	Stimulus	Criterion	Instruction
	0		
18(2)		31(1)	2
	21.5		
38(1)		45(2)	3
	43.5		
59(1)		57(1)	4
	64.5		
79(2)		74(4)	5
	84.5		
102(2)		92(4)	6
	107		

Note—Criterion levels are defined as normal deviates by $z(i|0) = -z(i|T_j)$, i.e., the intercepts of the ROC lines with the descending diagonal. Using the power function transformation fitted to the $d'(T)$ vs. T plot, criterion levels may be expressed in milliseconds. Left: data from Discrimination Instruction 1, using five criterion levels. Right: data from yes-no Instructions 2 to 6, using a single criterion level for each.

the detection-theoretical concept of the detection index being invariant for shifts of the criteria. Such shifts were induced by different instructions to discriminate the same set of six stimulus intervals, T_0 through T_5 , ranging from 0 to 107 msec. Six different instructions were used. Instruction 1 represents a rating instruction with six response categories, whereas Instructions 2 to 6 represent yes-no instructions. In the latter, the subject was asked to decide between category T_0 to T_{i-2} and T_{i-1} to T_6 for instructions (i), $i = 2, 6$. Figure 3 illustrates the resulting detection indices, d' , for all conditions. Only Instruction 2 and 6 show departures, due to the very extreme criterion settings (see Table 1). Note, however, the correspondence between criterion settings for Instructions 1 and 2 through 6.

Experiment 2 (Observers T.S. and W.O.) contributes to the above evidence in shifting the criteria by changing instruction, stimulus values, or stimulus a priori probability of occurrence, again leaving the acuity invariant among conditions. Shifts of the criteria, as induced by a change in stimulus probability of occurrence from equal probability for all four values to 50% for the zero stimulus and 16% for the other three, nevertheless amount to about 5 msec on the average. Table 2 summarizes the results. Observer T.S. performed both yes/no and rating instructions, while observer W.O. made only the yes/no conditions. All conditions combined with a stimulus series of either 0, 10.2, 20.5, 29.3 msec or 0, 15.5, 30.5, 50.8 msec. As can be seen from Table 2, only the factor "observer" provides for a significant source of variance.

Figure 4 presents two ROC lines and detection curves obtained from observer T.S. with a discrimination instruction and the set of large stimulus intervals. Both differ in the probability of occurrence of the individual stimulus values, as indicated. As suggested by Table 2, all detection indices obtained from observer T.S. are to

Table 2
Analysis of Variance of Criterion-Shift Experiments of the
Temporal Acuity Values A Obtained with Fixed Power Fitting
Procedure for the Combination of Conditions Indicated

Source of Variance	F Ratio	df	
Stimulus Probability of Occurrence	.35	1,7	$p > .5$
Stimulus Series	2.2	2,7	$p > .1$
Observer + Instruction	11.8*	2,7	$p < .01$
Observer	15.3*	1,4	$p < .05$
Instruction	.01	1,4	$p > .5$

*Significant.

Figure 4. ROC lines (top) and detection curves (bottom) obtained from a criterion shift experiment; Observer T.S. Left: Equal probability of occurrence for all four stimulus values. Right: Zero stimulus occurs with probability 1/2, the other three each with probability 1/6. Detection indices are fitted here with one power function (4), $A = 0.028(6)$ msec, $R = 1.32(6)$.

be fitted by one power function (4), which is shown in the figure.

These results lead to the conclusion that, in order to obtain the most reliable acuity values, stimulus values may be chosen so as to yield acceptable FA and hit rates without thus violating the consistency of the results. It is important to emphasize that it is the definition of a stimulus-independent acuity that enables this experimental freedom of design.

EXPERIMENT 3

Procedure

The spatial aspects of stimulus perception were investigated in Experiment 3 (Observer J.K.). The stimuli were presented, monoptically as well as dichoptically, as 1 out of the 10 possible pulse configurations depicted in Figure 5. The left eye was stimulated at 70' (300 μ m), either nasally or temporally, while the right eye received a pulse at -210', -140', -70' (temporally), 70', or 140' (nasally). Hence, it occasionally happened in the dichoptic case that the leftmost flash in the visual field was given

to the right eye, and vice versa. The observer could not, however, detect this without closing one eye. Depending on the expected acuity, two stimulus series were used, either 0, 16.2, 32.5, 43.5 msec or 0, 16.2, 32.5, 53.5 msec, both of which define four response categories. Irrespective of the stimulus configuration, for a nonzero stimulus the leftmost pulse in the visual field was always presented before the rightmost pulse. The duration of the pulses in these experiments was 8 msec at zero log intensity. Each stimulus interval for each condition was judged at about 250 trials, which amounts to 1,000 trials per condition.

Results

Figure 5 presents the detection curves for all geometrical conditions. The detection indices $d'(T)$ are

Figure 5. Schematic drawing of perceived stimulus geometry (center), and detection curves obtained for monoptic (left) and dichoptic (right) viewing; Observer J.K. T and N denote the areas in the visual field that project to the temporal and nasal semiretina, respectively. In monoptic viewing, the right eye was used. In both cases, the direction of the temporal interval was from the leftmost to the rightmost in the visual field. Detection indices are fitted with power functions with fixed exponent, $R = 1.58$, $\chi^2 = 55$ at 39 df.

Table 3
Analysis of Variance of the Geometry Experiment 3 of the Temporal Acuity Values A Obtained with a Fixed Power ($R = 1.58$) Fitting Procedure [$\chi^2(39) = 55$], and of the Raw Detection Indices d' (T)

Source of Variance	Significance Level	Test Parameter	
		Acuity A	d'
Monoptic/Dichoptic	Nonsignificant	$F(1,13) = .15$	$F(1,50) = .61$
Site Right Channel	Highly Significant	$F(4,13) = 3.8$	$F(4,50) = 8.3$
Site Left Channel	Poorly Significant	$F(1,13) = 1.6$	$F(1,50) = 7.0$
Distance Right-Left	Highly Significant	$F(7,11) = 4.5$	$F(7,47) = 9.0$

Note—The “distance” source of variance is obtained by sorting out the parameter values as to a constant value of the vectorial distance of both channels sites of stimulation. Degrees of freedom for the F ratios are in parentheses.

fitted by a power function (4), where a value of the exponent $R = 1.58$ was found to yield the best fit for all detection curves with different acuities, A. Analysis of variance is applied to two measures: to the acuities and to the detection indices d' . The results are presented in Table 3. From this table it may be concluded that the type of stimulation, whether monoptic or dichoptic, is not significant for the system. Furthermore, the spatial separation between flashes tends to be more significant than the site itself, though this is not very marked. Indeed, analysis on the basis of the detection

indices d' (T) fully confirms the results gained from the analysis of the acuities deduced from the fitted power functions.

Figure 6 gives the actual values of the temporal acuity, A. The most prominent feature is the dip in the case that both pulses are projected onto the same site, whether monoptically or dichoptically. Because monoptic and dichoptic results do not differ significantly, we conclude that the two flash signals fuse centrally before they actually are processed as to their time difference. This suggests that such signals first arrive at binocularly activated general centers before being processed by a specialized network.

Another phenomenon is the nonsymmetry for left and right hemispheric projections of the right pulse (Figures 6A and 6B). Clearly, this cannot be due to the stimulus polarity, i.e., the direction of the apparent movement, as that always is from left to right. Neither can there be a major effect of inward/outward movement asymmetry, as, for example, conditions that have a monoptically temporal-inward movement, in the dichoptic case change to right-temporal-inward and left-nasal-inward. Many such alterations may be constructed from Figure 5. Since no monoptic/dichoptic difference in performance was found, some effect of the stimulation site must be responsible. Two possibilities may be distinguished: projections either onto different semiretinae or onto different hemispheres. The data were therefore searched for those stimulations with both pulses projecting either onto the temporal or nasal semiretina or onto the left or right hemisphere, averaging over the same set of spatial distances and discarding the difference between monoptic and dichoptic stimulation. Each of the averages then results from four to eight measured values. As to the effect of semiretinae, the case in which both pulses are projected either temporally or nasally yields acuity values of $0.0291(8) \text{ msec}^{-1}$ and $0.0378(14) \text{ msec}^{-1}$, respectively (spatial distances 0' through 210'). As to the effect of hemispheres, when both pulses are projected either to the left or to the right one, acuity values obtained are $0.0330(12) \text{ msec}^{-1}$ and $0.0314(10) \text{ msec}^{-1}$, respectively (spatial distances 0' and 70' only). We conclude that pulses projected to the temporal semiretina yield a significantly poorer acuity than nasally projected pulses. The influence of

Figure 6. Summary of the temporal acuity values obtained from Experiment 3. Symbols: $\circ$, monoptic; $\bullet$, dichoptic; $+$, average of both. Site of the pulses in the fused visual field is relative to the fixation mark: negative, to the left; positive, to the right. Left and right channel refer to the dichoptic presentation only. The obtained acuity values are plotted vs. the site of the right-channel pulse. In (A) the site of the left-channel pulse is $-70'$ (cf. the upper half of Figure 5), and in (B) $70'$ (cf. the lower half in Figure 5). In (C) the separation between the pulses is plotted on the abscissa. For discussion, see text.

Table 4
Acuity Values Demonstrating the Influence of Spatial Separation of Pulses and Their Projections Onto Different Hemispheres (0' and 70' Data Used) and Semiretinae (0' through 210' Data Used)

Spatial Separation	Acuity	Projection		Acuity
0	.0291(9)	Hemisphere	Left	.0330(12)
70	.0388(14)		Right	.0314(10)
140	.0352(12)	Semiretina	Temporal	.0291(8)
210	.0300(9)		Nasal	.0378(14)

Note—Data averaged over monoptic and dichoptic presentation. Spatial separations are presented in minutes of arc.

Table 5
Temporal Acuity Values in msec⁻¹ Obtained by Fitting to the Detection Indices
for Each Condition a Power Function (4) with Fixed Exponent R

Intensity	Duration	Observer J.K. [R = 1.66; overall χ^2 (119) = 136]					Observer W.O. [R = 1.52; overall χ^2 (119) = 228]				
		Angular Diameter					Angular Diameter				
		3.5	7	14	28	56	3.5	7	14	28	56
0.0		.032(3)	.033(3)	.040(3)	.043(4)	.060(5)	.023(1)	.028(2)	.035(2)	.037(3)	.046(3)
-.6	8	.031(4)	.029(2)	.035(3)	.037(3)	.043(4)	.015(1)	.020(1)	.026(2)	.032(2)	.043(3)
-1.2		.026(2)	.029(2)	.038(4)	.040(4)	.041(4)	.013(1)	.016(1)	.024(1)	.030(1)	.031(2)
-.6		.036(3)	.039(3)	.045(4)	.043(4)	.053(4)	.021(1)	.030(3)	.034(3)	.045(5)	.042(2)
-1.2	32	.029(3)	.031(3)	.038(3)	.037(3)	.044(4)	.016(1)	.024(1)	.032(2)	.035(2)	.038(2)
-1.8		.023(2)	.029(3)	.034(3)	.038(3)	.039(3)	.014(1)	.014(1)	.023(1)	.027(2)	.031(2)
-1.2		.028(2)	.032(3)	.034(3)	.039(3)	.044(3)	.020(1)	.022(1)	.025(1)	.033(2)	.039(2)
-1.8	126	.026(2)	.029(2)	.033(3)	.040(4)	.042(4)	.012(1)	.020(1)	.026(2)	.026(1)	.032(2)
-2.4		.019(1)	.023(2)	.030(2)	.033(2)	.041(3)	.013(1)	.017(1)	.020(1)	.022(1)	.024(1)
-1.2		.032(3)	.030(3)	.028(2)	.035(2)	.040(3)	.019(1)	.021(1)	.027(1)	.028(1)	.037(1)
-1.8	500	.024(2)	.028(2)	.031(3)	.033(2)	.037(3)	.018(1)	.016(1)	.024(1)	.024(1)	.031(2)
-2.4		.022(2)	.027(2)	.026(2)	.035(3)	.032(2)	.013(1)	.015(1)	.020(1)	.026(2)	.027(1)

Note—Intensity is given in log units, duration in milliseconds, and angular diameter in minutes of arc. Constant pulse energy is found along the negative diagonal of the table for each duration.

spatial separation is visualized in Figure 6C. The presented data are summarized in Table 4.

EXPERIMENT 4

This experiment was designed to compare the limits for spatial and temporal integration for, say, the "brightness" and the "temporal acuity" channels. According to psychophysical evidence, foveal spatial integration under photopic conditions, as far as brightness discrimination is concerned (i.e., Ricco's area), amounts to only about 5' under brightness threshold conditions (Kulikowski & King-Smith, 1973; Thomas & Shimamura, 1974; Westheimer, 1967).

Procedure

In our experiment (Observers J.K. and W.O.), both pulses were presented 70' nasally to the dark-adapted eye. They were simultaneously varied with respect to intensity, angular diameter, and duration. These three measures constitute the total energy of a pulse of light. Intensity, i.e., the luminous energy per unit area per unit time in the retinal image, was regulated by neutral density filters. Each of four duration settings (8, 32, 126, or 500 msec) was paired to each of five angular diameters (3.5, 7, 14, 28, 56' of arc, i.e., 15 to 240 μ m of retinal diameter) at three levels of intensity, spaced in 0.6 log unit intervals. The latter were chosen 0.6 log unit lower at each set of points with a longer duration (except for the 500-msec combinations) so as to keep the brightness within reasonable bounds. Thus, pulse energies—but not brightness—range over 4.2 log units. An overview of the conditions and the obtained acuity values may be found in Table 5 for both observers, J.K. and W.O. For each condition, 1,000 trials were presented.

Results

Angular diameter. In foveal vision, total spatial summation according to Ricco's law is demonstrated for very small test fields only, of the order of several minutes of arc (e.g., Westheimer, 1967). This result, however, applies to measurements of brightness threshold. There is no a priori reason to exclude total or partial

summation if neural information encoding a pulse of light is processed in a different way according to a different question being asked of the observer.

To further analyze the data with respect to the dependence of temporal acuity on the angular diameter of the pulses, we averaged the data over different settings of intensity and duration, for fixed values of angular diameter and total pulse energy.

The obtained values are plotted in Figure 7 for both observers. The five sets of points having the angular diameter as a parameter are shown to yield a single line vs. log energy. This means that increasing the angular diameter of the pulses in the range indicated is

Figure 7. Temporal acuity values as a function of the pulse energy averaged over the pulse durations of 8, 32, and 126 msec, with the angular diameter as a parameter. Observers J.K. and W.O. Dashed lines fitted according to Equation 5.

equivalent to increasing other parameters constituting total pulse energy. Hence, with respect to temporal acuity, full spatial summation occurs up to at least 1° in the fovea.

Pulse duration. Above we found complete spatial summation for all angular diameters used. Hence, in searching for the effect of the pulse duration, we may average the data over different settings of intensity and angular diameter for fixed values of pulse duration and total pulse energy. In Figure 8, the resulting values of temporal acuity are plotted logarithmically vs. log pulse energy.

The heavy lines connecting points of constant "energy per second" as defined by intensity and angular diameter, but differing in pulse duration, reveal that full temporal summation occurs up to at least 32 msec, whereas longer durations branch off the main line. This main line represents the dependency of temporal acuity, A , on pulse energy, E , as long as pulses may be regarded as spatial and temporal δ pulses (i.e., pulses with vanishing duration, but nonvanishing time-intensity integral) with respect to the mechanism of temporal acuity. It is established that this relationship may be represented by the power function:

$$A(E) = K \cdot (E/E_r)^r, \quad (5)$$

where K and r are parameters to be determined. Their values are given in Table 7. E_r is a scale factor that, with our arbitrary energy units, will be taken as unity. Following the heavy lines, again it may also be inferred from Figure 8 that increasing the pulse duration beyond the limit of summation tends to reduce temporal acuity instead of further enhancing it or making it follow a saturation curve.

EXPERIMENT 5

There is evidence that, at increasing adaptation levels, the response of the visual system to pulses of light decreases in duration and latency. In a dichoptic Pulfrich experiment, Rogers and Anstis (1972) measured latency differences and by deduction calculated true latencies. Over 5 decades of surround luminance, they established a power relation with exponent -0.2 , corresponding to a latency decrease from 150 to 5 msec. In accordance with these results, Mansfield (1973), in foveal reaction time experiments, found a power relation with exponent -0.3 . Matteson (1971), in a dichoptic perceived-order experiment, reported a difference in latency in the fovea of 100 msec over a range of surround luminance from 0 to 5 log trolands. Over the same range, Prestrude (1971), in a dichoptic rotating Pulfrich experiment, found a decrease of only about 40 msec. Good correspondence between the results obtained by different methods was established by Roufs (1974), who performed reaction time and perceived order experiments, the latter also between a visual flash and an auditory click. The results of these experiments differ only in an additive constant,

Figure 8. Temporal acuity values as a function of the pulse energy averaged over all angular diameters with the pulse duration as a parameter. Observers J.K. and W.O. Dashed lines are fitted according to Equation 5; values of the parameters is given in Table 7. Heavy lines connect equal "energy-per-second" points.

representing different information conduction times.

From the well-known De Lange characteristics (De Lange, 1957; Kelly, 1971a, 1971b), if we tacitly interpret them as frequency transfer functions of a specific visual pathway, we may infer that at increasing adaptation level the response to a short pulse indeed becomes shorter in duration and more biphasic (as equivalent to the shift of the peak sensitivity to higher frequencies combined with the increasingly pronounced low-frequency cutoff), but also smaller in amplitude (as equivalent to the decrease in sensitivity in the low-frequency limit). This argument, however, applies only to a very specific pathway, which need not necessarily be the same as that used in other perception tasks.

These changes in response, both in latency and in amplitude, may have their impact upon the signal-to-noise ratio of the responses which limits temporal acuity.

Procedure

In our experiment (Observers J.K. and J.W.H.), a constant adapting field, on which the stimulus pulses were superimposed, was used equally in both eyes. The pulses were of 8 msec duration, and $14'$ angular diameter, and were presented $70'$ nasally. Their intensity was set from 0 to -2.4 log units in steps of 0.6 log units on the same scale as used in Experiment 4. From this, we conclude that full spatial and temporal summation should occur. Hence the relevant measure is pulse energy, which, on the same arbitrary scale as in the above experiment, ranged from -1.2 to -3.6 log units.

The adapting field was seen in Maxwellian view at angular diameters of approximately 8° , 16° , or 24° . It was set at four different intensities, decreasing in 0.6 log unit steps. Several series of control trials without adapting field, i.e., under conditions equivalent to some in the previous experiment, were presented intermingled with the other parameter settings throughout all sessions. Only the lower pulse energies were presented at the lower field intensities so as to remain well above the brightness increment threshold. Table 6 presents an overview of the conditions and the resulting acuity values for both observers, J.K. and J.W.H., who both again judged 1,000 trials per condition.

Table 6
Temporal Acuity Values in msec⁻¹ Obtained by Fitting to the Detection Indices
for Each Condition a Power Function (4) with Fixed Exponent R

FD	PE	Observer J.K. [R = 1.42; overall χ^2 (93) = 64]					Observer J.W.H. [R = 1.23; overall χ^2 (93) = 113]				
		Field Intensity					Field Intensity				
		$-\infty$	-1.8	-1.2	-.6	0	$-\infty$	1.8	1.2	-.6	0
8			.043(4)	.042(3)	.047(5)	.043(4)		.028(2)	.025(2)	.027(2)	.024(2)
16	-1.2	.041(3)	.043(4)	.046(5)	.043(4)	.046(6)	.028(2)	.023(2)	.028(3)	.029(3)	.028(2)
24			.045(6)	.051(6)	.048(6)	.041(4)		.022(1)	.020(1)	.029(2)	.025(2)
8			.042(4)	.042(4)	.046(6)	.051(10)		.022(2)	.026(2)	.024(2)	.018(1)
16	-1.8	.041(4)	.046(5)	.039(4)	.039(4)	.045(8)	.020(2)	.023(2)	.030(3)	.028(3)	.020(2)
24			.040(4)	.047(5)	.043(4)	.047(7)		.017(1)	.018(1)	.020(1)	.021(1)
8			.043(5)	.044(7)	.039(5)			.017(1)	.021(2)	.018(1)	
16	-2.4	.037(3)	.036(3)	.045(7)	.042(7)		.020(1)	.019(1)	.027(3)	.028(3)	
24			.035(5)	.038(5)	.043(5)			.016(1)	.018(1)	.019(1)	
8			.038(6)	.033(3)				.018(1)	.018(1)		
16	-3.0	.038(5)	.041(6)	.037(4)			.015(1)	.021(2)	.017(1)		
24			.031(3)	.037(4)				.017(1)	.014(1)		
8			.031(3)					.013(1)			
16	-3.6	.028(3)	.030(2)				.011(1)	.013(1)			
24			.019(3)					.009(1)			

Note—FD = field diameter in degrees; PE = pulse energy in log units. Field intensity is given in log units; field intensity $-\infty$ denotes the near dark-adapted state.

Results

Field intensity. We first turn our attention to the influence of adapting field intensity on temporal acuity. As all combinations of field intensity and pulse energy are presented with all three field diameters, we first average the data over these diameters. Figure 9A presents the resulting acuity values vs. log field intensity with pulse energy as a parameter. It can easily be seen that, for both observers, the acuity does not depend on the field intensity. If there were any effect, then we would expect a decrease in acuity, which certainly is not demonstrated. Yet, the data are not conclusive enough to suggest a tendency for acuity increase. Therefore, we are forced to conclude that, in the presence of an adapting field, temporal acuity is independent of the resulting adaptation level within a reasonable range, including dark adaptation.

Field diameter. As no effect of field intensity is found, we may average the data over this parameter and plot the resulting temporal acuity values vs. the field angular diameter, with the pulse energy as a parameter. Figure 9B thus should exhibit the influence of field diameter on acuity, if present. One has to conclude that field diameter also has no appreciable effect on acuity, thus supporting our conclusion as to field intensity. For small diameters, the data are continuous with the values obtained from dark adaptation, plotted at zero diameter. Only at large diameters is there a slight indication of a decrease in acuity. We may now plot the data of Figure 9A vs. log pulse energy to compare the results with those from the previous experiments. Figure 10 shows that the data obtained at various light-adapted conditions just scatter about those obtained in the dark-adapted state. As indicated, the experimental points at all field intensities may be fitted by the power

relation of Equation 5. The values of the parameters are given in Table 7.

POWER VS. LOGARITHMIC RELATION

The dependence of acuity, A , on the pulse energy, E , as shown in Figures 7, 8, and 10, may be represented by a power as well as by a logarithmic relation:

Figure 9. (A) Temporal acuity values as a function of adapting field intensity averaged over all field diameters with the pulse energy as a parameter. (B) Temporal acuity values as a function of adapting field diameter averaged over all field intensities with the pulse energy as a parameter. Observers J.K. and J.W.H. The leftmost points in each plot represent the results from the dark-adapted control experiment.

Figure 10. Temporal acuity values as a function of the pulse energy averaged over all adapting field diameters with field intensity as a parameter. Observers J.K. and J.W.H. Dashed lines are fitted according to Equation 5; values of parameters given in Table 7.

$$A(E) = K \cdot (E/E_r)^r \quad (5)$$

and

$$A(E) = C \cdot \log E/E_0 \quad (E > E_0), \quad (6)$$

where E_r is a scale factor, arbitrarily set to unity. Table 7 gives the values of the parameters for both functions.

It can be seen that a preference for one of these relations cannot be based on goodness of fit, as they yield practically equal chi-square values. In Equation 6, the relative values of E_0 , interpreted tacitly as an energy threshold for the temporal acuity mechanism, should correspond to differences in brightness threshold between observers up to about 2 log units. However, the photopic thresholds for all three observers were found to be identical with 0.2 log units. Hence, as E_0 cannot be interpreted consistently, we prefer the power relation of Equation 5.

DISCUSSION

As stated above, the existence of normal distributions in the detection process is verifiable by means of the experimentally obtained ROC curves. Though each ROC line fitting in most cases leaves only 1 degree of freedom, for all experiments reported, the great number of these adjustments yields sufficient evidence to conclude, indeed, the normality of the distributions encountered, due to an overall chi square of 716 with 702 degrees of freedom. By manipulating the observer's criterion, results were found which are consistent with detection theoretical concepts.

Temporal acuity was defined by a simple power relation, as expressed in Equation 4, which proved to fit the detection index data in general very well. A linear function, which would necessitate the assumption of a threshold at about 10 msec, was rejected because of its poorer fit ($\chi^2 = 652$ vs. $\chi^2 = 547$ for the power relation, with 428 degrees of freedom, determined from Experiments 4 and 5). By using Equation 4, an important data reduction is obtained, where the exponent R may be held constant for all data from one observer's experiment.

Geometry

Projecting the pulses of light on different locations in the visual field does affect the sensitivity of the mechanism (Experiment 3). For foveal stimulation, the spatial separation of the flashes seems to be more impor-

Table 7
Obtained Parameter Values by Fitting a Power or a Logarithmic Relation to the Acuity vs. Pulse Energy Data

Observer and Condition	df	$A = K \cdot (E/E_r)^r$			$A = C \cdot \log E/E_0$		
		K	r	χ^2	C(msec ⁻¹)	log E_0	χ^2
W.O.	8 + 32 msec	.050 (1)	.157(4)	62	.0084(2)	-5.1(2)	64
	126 msec	.0384(9)	.133(5)	29	.0062(2)	-5.5(2)	39
	500 msec	.0299(5)	.117(5)	13.2	.0055(2)	-5.3(2)	20.6
J.K.	8 + 32 msec	.051 (2)	.085(7)	12.7	.0068(6)	-7.2(6)	13.0
	126 msec	.048 (2)	.099(8)	7.7	.0071(5)	-6.5(5)	1.65
	500 msec	.035 (1)	.063(8)	4.9	.0042(5)	-8.4(1.1)	5.45
J.K. all fields	17	.055 (2)	.073(8)	16.0	.0072(7)	-7.4(7)	26
J.W.H. all fields	17	.0341(9)	.114(5)	101	.0049(2)	-6.1(3)	83
Overall χ^2	78			246			253

Note—Conditions refer to the pulse durations of the pulse energy experiment, and "all fields" denotes the data from the adapting field experiment averaged over all field conditions.

tant than their location. Results from monoptic as well as dichoptic spatially homonymous flashes indicate that the processor P (cf. Figure 1) receives information that already is binocularly integrated.

There is experimental evidence that each hemisphere is specialized in certain complex perceptual tasks. The processing of language material would be confined to the left (dominant?) hemisphere, while depth perception mainly is achieved by the right one (Durnford & Kimura, 1971). Corwin and Boynton (1968) and Efron (1963) have argued from their data that a common "simultaneity center" for all sensory modalities possibly is located in the dominant hemisphere. If this is true, then information projected onto the right hemisphere must have at least one extra neural stage to go through, and hence may end up with a greater variability than information projected directly onto the left hemisphere. This effect would lead to a lower "noise level" of signals after being transmitted through the left hemisphere than through the right one, hence to a higher temporal acuity. The data are not in conflict with these findings, as the observer is right-handed (cf. Efron, 1963).

The most pertinent finding from this experiment is, however, that signals transmitted through the temporal semiretinae have about 20% poorer signal-to-noise ratios than those transmitted via the nasal ones [acuity $0.0291(8) \text{ msec}^{-1}$ and $0.0378(14) \text{ msec}^{-1}$, respectively], as measured through our temporal acuity system. This effect describes the asymmetry in Figure 6. It is paralleled by, but not logically connected to, Poffenberger's finding (1912), as cited by Efron (1963), that stimulation of the temporal semiretinae results in longer reaction times than if the nasal ones are stimulated. However, possible latency differences between hemispheres or semiretinae would not have been revealed by our type of experiment.

Pulse Energy

Evidence is given that the temporal acuity mechanism makes use of grossly integrated visual information, especially in the spatial domain. We do not know of psychophysical experiments where spatial information in the fovea is actually perfectly summated to the extent of 1° of visual angle, thus enhancing a detection task in the same sense as the intensity does. However, receptive fields of single cortical cells in the monkey, especially the feature-detecting complex and hypercomplex cells, tend to be much larger (Hubel & Wiesel, 1968) than psychophysically determined foveal integration areas (Westheimer, 1967).

Flicker sensitivity with sinusoidal bar patterns (Kelly, 1972) yields maxima at 1 to 2 c/deg of spatial frequency, indicating receptive fields of the same order of magnitude as are found here. The range of temporal integration found is not surprising, as it is well within the range of values found to apply to Bloch's law. Such integration in time, however, cannot exist unless there is a decay in time to prevent a blowup of the system.

Tittarelli and Marriott (1970) tried to describe threshold behavior with an exponential decay. This hypothesis works very well to describe the threshold of a double pulse but fails in the case of a long-duration continuous pulse. Nevertheless, for the foveal threshold, an integration decay constant of about 25 msec could be established. Above threshold, under suppositions of linearity, from the high-frequency cutoff of flicker fusion characteristics (De Lange, 1957; Kelly, 1971a, 1971b) of about 10 to 20 Hz, an estimate for an integration time constant of less than 15 msec can be derived.

Thus our temporal integration, in fact, outranges somewhat the one governing brightness (increment) detection, indicating that still some integration may take place more centrally, as, in fact, it does in the spatial domain.

The increase of acuity with increasing pulse energy should somehow be paralleled by a change in the neural pulse response amplitude. In many cases, the latter was found to be a logarithmic function of pulse intensity (Campbell & Maffei, 1970; Fiorentini & Maffei, 1973).

When logarithmic relations are found, the rise in amplitude is mostly rather steep, leading to a saturation level in 1 or 2 decades of stimulus intensity (Fiorentini & Maffei, 1973; Thorn, 1974). On the other hand, Suzuki, Nunokawa, and Jacobson (1972) found, in the cat's cortex, only a very slight dependence of the amplitude of the VEPs (which were of very complex nature) on the magnitude of large field intensity increments over many decades; rather, it was the *form* of the response that changed.

In other experimental conditions, the amplitude of the neural response shows an approximately linear relation to the intensity of the stimulating pulse of light, though in a small range only. Peck and Lindsley (1972) recorded evoked potentials in the cat from the optic tract, the lateral geniculate body, and the striate cortex elicited by paired pulses. These VEPs added fairly linearly up to an interpulse interval of about 80 msec (LGB) or 100 msec (cortex). Beyond 100 msec, cats were able to discriminate faultlessly between single and paired flashes. Below 100 msec, the percentage of responses to "paired flashes" gradually falls to a false positive rate of about 20%. Ter Laak (1975) found, in the *Tupaia* optic tract, a linear relation between (single) pulse intensity and the number of extra spikes in the burst above the maintained activity. As no clear threshold was found, an intensity range where this linear relation holds is difficult to define, but probably will not exceed 1.5 decades. Linearity therefore does seem to prevail only in rather peripherally located single cells (fibers) and over only a small range of intensity while more centrally located and more global responses seem to follow a logarithmic (or power?) relation. Hence, it seems unlikely that higher perceptive functions, working over a large range of stimulus intensity, will show a linear dependence on that intensity.

In our experiments, an increase of pulse energy over more than four decades (not yet leading to saturation)

results in only a small increase in acuity of about a factor 2 to 3. Though the retinal illuminance varies over a smaller range, this still amounts to 2.4 log units, which is the upper limit of the dynamic range given in the studies mentioned above.

Adaptation

We found temporal acuity to be independent of the presence of an adapting field from about 2.5 log units above photopic threshold down to a rather dark-adapted state. This is best demonstrated by comparing the results of Experiments 4 and 5 for observer J.K. for the 8-32-msec and the "all fields" conditions, respectively. They yield relations between acuity and pulse energy which are equal within experimental error (cf. Table 7). To infer the physiological meaning, two aspects must be kept in mind: the direct effect of adaptation on the amplitude and time scale of the pulse response and the effect of signals elicited by the field itself.

So far, there is little conclusive electrophysiological evidence for the influence of adapting light on responses to pulses of light. Samson and Young (1973) found, in the pigeon's optic tectum, a decrease in amplitude and, surprisingly, an increase in latency for the pulse response at increasing background luminance. Suzuki et al. (1972), on the other hand, in the cat's cortex and with luminance increments at very large fields, recorded VEPs that, in amplitude, were fairly independent of both increment luminance and adaptation level; instead, these parameters influenced latencies and relative dominances of individual parts of the VEP. The effect of adaptation level was followed over about 3 decades. The only evident change to be found in the VEP was the rather abrupt vanishing, part by part, of the increment response as luminance increment decreased below a certain value. They defined this value as the critical luminance increment, which, as a function of adaptation luminance, followed a Weber law. The Weber constant was found to be in good agreement with values determined psychophysically under the same experimental conditions.

On the other hand, for the transmittance of transient and sustained information, separate channels have clearly been shown to exist in the cat from the retinal ganglion cells up to cortical levels (Cleland, Dubin, & Levick, 1971). Here the transient neurons do not respond to a steady illumination, whereas the sustained ones, of course, do. The latter respond to increments as well, although less so than the transient neurons. The distinction further is characterized by the fact that transient channels have smaller latency, shorter pulse response (as derived from a spike poststimulus time histogram; Cleland, Levick, & Sanderson, 1973), and less latency variance, properties all especially suiting these channels for the transmission of temporal information.

Evidence exists that such separate channels are to be found in primates too. In the Tupaia, which possesses an all-cone retina, Ter Laak (1975) found in the optic tract units exhibiting roughly the above mentioned

characteristics. Furthermore, spatial differences seem to exist in that the sustained cells were found to prevail in the retinal area centralis and that transient cells are to be found in the contralateral optic tract only. As a function of adaptation, both units proved to change their sensitivity in the same way, but the burst duration appreciably decreased with increasing light adaptation in the sustained cells and remained virtually unchanged in the transient cells. The diameter of the uniform center (corresponding to Ricco's area) for the sustained units was practically independent of adaptation (about 1°), while in the transient units this diameter decreased from about 4° to 1° with increasing light adaptation.

If we suppose the sustained channels to be unemployed in temporal processes, then no extra noise is added to the relevant signals and the presence of an adapting field will only amount to a change in amplitude and time scale of the pulse response. This change will affect the detectability of the time intervals between pulses unless it is compensated by a change in temporal accuracy, say the variance of the latency, of the pulse response. So far, we know of no electrophysiological evidence to support or refute such views.

The complex nature of the mechanism of temporal acuity may be appreciated by considering the finding that increasing the duration of the pulses demarcating the stimulus time interval—thus leaving intensity and angular diameter unchanged (see the heavy lines in Figure 8)—tends to reduce the detectability. If simply some kind of time mark were taken from the leading edge of the response, then a leveling off to constant performance would be more likely. Obviously, the tails of the responses to pulses longer than about 150 msec are still able to disturb the signal-to-noise ratio. This, of course, is in conflict with the supposition made above, that only transient channels contribute information for temporal processing.

If, indeed, our conclusion that the presence of an adapting field does not influence temporal acuity is justified, one might wonder what consequences arise in relation to physiological evidence. Results exist (Coenen & Eijkman, 1972; Nikara, 1971; Samson & Young, 1973; Ter Laak, 1975) indicating that the amplitude of neural responses decreases with increasing adaptation level. If this is true, in order to maintain the same acuity, the relevant variance of the pulse response should decrease, too. To what extent it should decrease depends, of course, on the detailed action of a hypothetical processor, P, which delivers the acuity signal (cf. Figure 1).

It may be interesting to perform experiments in which the adapting field is switched off just before the stimulus pulses appear, so as to remove any effect of its presence other than setting the adaptation level, or, the other way round, to switch the field on only shortly before the appearance of the stimulus pulses, thus maintaining a low adaptation level. Such experiments may, however, be quite troublesome in view of the temporal relations between the onset of field and

pulses. Under conditions where the adaptation light was switched off just before the onset of flashes, Thijssen (1969) did experiments on brightness detection and discrimination of flashes. No marked effect of the adaptation level and the presence or absence of a background field on the relevant noise was found.

About the absolute values of the mean and standard deviation of the relevant neural signal $X(T)$, no explicit statements can be made. However, it is known from other investigations that the response to a single pulse of light already exhibits some variability. Zacks (1973) has estimated the variability of the latency of responses to brief pulses. This he achieved by asking the observer to indicate *which one* of two spatially separated but otherwise identical pulses was presented first. For flashes of a brightness comparable to ours, he obtained a standard deviation of 13.5 msec for the distribution of response latencies. When two such independent variabilities form the input to the time interval processor that we hypothesize, the standard deviation $\sigma(T)$, if we take it to be equivalent to a time domain measure, should at least amount to $13.5\sqrt{2} = 19$ msec. Due to the nonlinear relationship between the time domain stimulus and the processor output, such equivalencing is not strictly admissible. An estimate of $\sigma(T)$ can be derived from the temporal acuity values yielded.

It was stated before that A equals the inverse stimulus T that yields a detection index d' of unity. Then according to Equation 3, the internal signal $X(T)$ due to T on the average is increased by $\sigma(0)$. Thus, $\sigma(0)$ may, in the temporal domain, roughly be taken equivalent to A^{-1} . Values obtained under conditions comparable to those of Zacks amount to about 30 msec. Under optimal conditions, minimum values of A^{-1} of about 20 msec are reached. Thus, it may be concluded that latency variability is included in the results presented here.

The values obtained for the temporal acuity, A , in our experiments range from 0.02 to 0.06 msec⁻¹. From these data, it follows that time intervals of the order of 50 μ sec (von Békésy, 1969) may at the very best reach a detection index d' of 0.003. In the latter experiment, however, a moving target was used with much more information than is present in our stationary flashes and empty intervals.

On the other hand, determinations of the stimulus interval in which the flashes are perceived as being just adjacent in time (Efron, 1970) yield magnitudes out-ranging ours. Efron, using parafoveal binocular stimulation with flashes purposely differing in brightness and color, found that if the first pulse is shorter than 90 msec (!) one can obtain values for the pulse interval of about 230 msec. Even an analogous experiment in audition yields a click interval of 175 msec. According to our data, such an interval ($d' = 8$) should be easily discriminable from simultaneity, where an interval of about 50 msec reaches $d' = 1$ at about the same retinal positions. Results obtained by Ross and Hogben (1974) about the temporal lag allowed between the presenta-

tion to both eyes of stereoscopic information tends to confirm our findings though their experimental aims were quite different.

It is our feeling that most of the numerical contradictions found imply that the quite different tasks imposed on observers may measure quite different physiological entities.

In summary, we conclude, from the experimental evidence presented here, that:

(1) The probability distributions encountered may be considered normal.

(2) A set of d' values obtained from one observer for every condition obeys a power law with a fixed exponent and with the so defined temporal acuity as a parameter.

(3) Temporal acuity is invariant with respect to experimental procedures which otherwise might bias the observer's performance, e.g., by influencing his criterion setting.

(4) The mechanism for time interval discrimination receives information that is already binocularly integrated and may be confined to the left hemisphere. Pathways originating from the temporal semiretina introduce a poorer signal-to-noise ratio than those arising from the nasal semiretina. There is no evidence for any difference in behavior between monoptic and dichoptic stimulation.

(5) Variability of the latency of individual flash responses is not in conflict with the temporal acuity values obtained here.

(6) Temporal acuity for nonmoving patterns in vision (~ 0.05 msec⁻¹) is on the order of 200 times lower than temporal acuity in audition (~ 10 msec⁻¹).

(7) The temporal acuity mechanism, as a feature detector, enhances its performance by using foveally largely integrated visual information, spatially up to at least 56', temporally up to at least 32 msec.

(8) Within the bounds of integration, temporal acuity may be described by both a power and a logarithmic function of the integrated pulse energy.

(9) The mechanism is likely to use mainly information from so-called transient channels, as within reasonable bounds an adapting field is irrelevant to the mechanism.

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