On Gerald S. Wasserman and King-Leung Kong (1979) Absolute timing of mental activities. BBS 2:243–304.

Abstract of the original article: A new tool that may measure certain absolute temporal properties of information processing in intact organisms is suggested by investigations of temporal summation in single nerve cells. Two findings have led to this suggestion: One, the form of the temporal summation function (relating the intensity and duration required to evoke a criterion neural signal) depends on the analysis used by the investigator. Corresponding form variations occur in behavioral studies when the observer's task is varied. Two, the critical durations of fixed neural signals depend on the latency of the feature of the signal chosen as criterion; early features yield short critical durations and vice versa. The critical duration also varies in behavioral studies if one varies the observer's task, keeping the stimulus ensemble fixed.

These data lead to two inferences: One, the form of a behavioral temporal-summation function expresses the kind of hidden mental analysis mediating that behavior. Two, a behavioral critical duration is an indicator of the absolute timing of the hidden mental analysis mediating that behavior.

The timing of mental activities with nonvisual stimuli

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Wasserman & Kong's (1979) analysis of temporal summation in vision provides both a useful review of the relevant physiological and psychophysical literatures and an ambitious attempt to develop a model of human mental activity. The model suggests that the nature of the underlying integrative mechanism can be identified as involving a neural recoding, an event, or a process; it also claims to provide a means to determine the latency of the mental analysis – when an event occurs or a process ends. Both the paper and the subsequent commentaries seem to address the first issue more than the second, reflecting the paucity of those theoretical and empirical advances that will allow us to adjust critical durations by an invariant time period.

This commentary has three goals: to raise, briefly, a conceptual issue that deserves further attention; to add information relevant to the Wasserman & Kong (W & K) model; and to describe some experiments on temporal integration with electrocutaneous pulses that are directly pertinent to the distinctions (peripheral vs. central summation; events vs. processes) that the authors address.

W & K seek to relate psychophysical reports to the physiological signals that can be obtained from microelectrode recordings in preparations such as *Limulus*. Their linking hypothesis is that "similarities between the particular findings reported by a physiologist and the behaviors displayed by an intact organism imply corresponding similarities between the particular mental analysis in which the intact organism was engaged and the data-reduction analysis used by the physiologist." Accordingly, among their potential analysis options is a class labeled "latency," which includes the time from stimulus onset to the time of (i) some criterion amplitude of the receptor potential, (ii) some point in the first of a series of action potentials, or (iii) the peak frequency of spikes.

Various commentators (e.g., Marriott 1979; Treisman 1979; Wandell 1979; Yeandle 1979) have pointed out that analysis of the last sort ought to be considered a process rather than an event; my contention is that the first two analysis options present serious difficulties. Latency measures are easy for the

electrophysiologist to obtain – he has distinct markers of stimulus onset and the occurrence of the neural signal. The observer, however, except under highly artificial situations, has no basis for making a latency determination. This problem does not, in itself, rule out all event options since, for example, some criterion amplitude of a receptor potential can be detected by a mechanism that has no information about stimulus onset. However, Levick's (1979) concerns about the contributions of neural noise and maintained discharges mandate careful acceptance of this option as well.

W & K intentionally limit their examination to the visual literature. Several commentators (e.g., Babkoff 1979; Feth 1979; Raab 1979) suggest that there are potential parallels in the literature on auditory temporal integration, while others (e.g., Bibikov 1979; Posner 1979; Ventura 1979) emphasize some of the intersensory differences. Given the primary relationship between critical duration and reaction time in W & K's theory, one vitally important distinction has been overlooked. They find, in *Limulus*, that modification of a physiological response criterion generates a linear function relating critical duration to response latency. They indicate that they would be "exceedingly surprised if no such relation existed in man, for both the critical duration and the latency of visual responses have long been known to decrease as intensity increases." Mansfield (1979), Ueno (1979), and Weale (1979) refer to corroborative behavioral and neural data for the visual system. However, in audition, while increases in intensity yield decreases in reaction time, they do not yield decreases in critical duration (Stevens & Hall 1966). Similarly, Rollman (1974; 1975) found that critical duration for electrocutaneous pulses was equivalent at threshold and suprathreshold intensities. Babkoff (1978) reported evidence for increased critical durations at higher intensities of electrical stimulation; similar results for warmth have been noted by Marks and Stevens (1973).

W & K's inferences regarding the form and timing of the mental analysis mediating a behavior are indirect in that they are based upon observed parallels between neurophysiological data in *Limulus* and psychophysical data obtained almost entirely from man. Research in my laboratory has suggested that related information can come from direct psychophysical studies with human observers, using carefully controlled electrocutaneous stimuli to selectively tap differential peripheral and central functions. These data, too, demonstrate a wide range of critical durations for temporal summation, depending

upon the characteristics of the stimulus and, consequently, upon the site of information processing.

Studies on temporal summation, using single rectangular electrical pulses (Rollman 1969; 1974; 1975), showed that threshold current decreases with increases in stimulus duration. Complete reciprocity between intensity and duration extends to a critical duration (t_c) of only 80 μsec, a value several orders of magnitude smaller than those reported in other modalities. Beyond that there are two periods of partial summation, one extending to about 1.0 msec and another to 10.0 msec; and for longer pulse widths, threshold is independent of duration.

This pattern of complete and partial summation has since been determined to exist under a variety of dependent measures. Similar values of critical duration occur when one uses magnitude estimation, cross-modality matching, and response latency.

These psychophysical data yield functional relationships similar to those presented in Figures 2 and 5 of W & K's target article. They also match the strength-duration curves (Heckmann 1972; Wynn-Parry 1971) of large A-fibers obtained by electrophysiologists. Since the temporal parameter that describes those curves, the chronaxie, is similar in the psychophysical and neuroelectric determinations, the critical duration of 0.1 msec of less represents the sharply limited capacity of the peripheral nerve to integrate sensory information.

Electrical excitation of the nerve represents non-adequate stimulation; long values of t_c found in vision, audition, and other modalities (including vibration of the skin, Verrillo 1965) are obtained after presentation of signals that impinge upon sensory receptors. However, as W & K point out, "temporal summation is not determined by the receptor signal alone but instead depends on the analysis of the receptor signal as well." The long values of t_c in vision, for example, do not occur because photoreceptors integrate over lengthy periods; they arise from central interpretation of afferent information.

On the basis of this concept, I began (Rollman 1974) to examine temporal summation for more complex electrical signals (Gibson 1968; Hahn 1958; Uttal & Krissoff 1968), expecting to find that t_c would be greatly extended if trains of pulses, rather than single pulses, were employed. Thresholds were obtained for trains differing in pulse duration, pulse number, and stimulus-onset-asynchrony (SOA) (and, consequently, in total train duration and in integrated "on-time"). The interactions of these parameters are complex; essentially, threshold tends to decrease, within specified limits, with increases in pulse number and decreases in SOA.

When the SOAs are exceedingly short (under 1.0 msec), successive pulses produce neural effects that are not independent, since a stimulus may occur while the nerve is in an absolute or relative refractory period. Under these conditions, successive pulses have the effect of extending the duration of the electrical signal. The decreases in threshold for a train of pulses are equivalent to those that occur for the lengthening of a single pulse, and the temporal integration function continues to reflect peripheral processes.

As SOA is increased beyond 1.0 msec, the peripheral nerve fibers are entrained by the stimulus sequence (Buchthal & Rosenfalck 1966). Now, t_c is, in fact, increased dramatically, since threshold declines with increases in train duration up to 100-300 msec.

These results indicate an altered mode of signal analysis as the afferent signal changes from a single, synchronous discharge to a repetitive pattern of action potentials. Whereas the former engages a peripheral mechanism (which obviously has central consequences, involving spatial integration across a population of fibers, Rollman 1975), the latter creates a sequence of temporally dispersed neural events which are subject to the limitations of a central integrative process.

The data suggest that this central information analysis is based upon a combination of timing and counting components, in which the number of neural events occurring during a critical sampling period is paramount in determining threshold. Later experiments (Rollman 1979), involving loudness-matches to suprathreshold electrocutaneous pulses, demonstrated a similar process – over a range of SOAs, perceived magnitude increases as train duration is extended to about 100 to 300 msec; additional increases in pulse number (and, therefore, in time) have no effect. Furthermore, for durations less than the integration time, it is the number of events that is important – for 2 pulses, perceived intensity is independent of SOA as long as the total duration is within the specified range. The same is true for 4, 8, 16, or 32 pulses. Similar integrative periods were found in studies of masking (Rollman 1974) and two-pulse resolution.

The temporal summation results have an apparent resemblance to the function produced by W & K from a process analysis with a limited central integration period, with the exception that the electrocutaneous data do not exhibit "super-summation." But, unlike their model, the results do not emerge from an integration time "arbitrarily chosen"; they arise instead from direct consideration of the experimental outcome. It ought to be possible to let the data speak for themselves.

W & K's reliance upon reaction time data to reflect the critical duration for a mental process is also problematic. The results presented above show an enormous difference in t_c for single and repetitive electrical stimuli. However, tactile reaction times do not show appropriate differences.

Individual mechanical pulses, which stimulate cutaneous receptors, produce a series of action potentials, but the reaction times for subjectively equal electrical and mechanical signals are also equal (Rollman 1974). So, too, are the reaction times for single pulses and trains.

To retain the W & K model's reliance upon response latency, it may be necessary to invoke a neural event option for single electrical stimuli and a neural process option for pulse patterns. However, other interpretations, related to those offered by Sternberg (1979), are also possible.

In order to assess how adequately patterns of electrical impulses to the skin mimic central neural events, it is instructive to examine the literature on direct cortical stimulation. Libet (1973) found that the critical duration for a train of electrical pulses presented to the somatosensory cortex was around 500 msec; although he reported that t_c for a train to the skin was only 100 msec, longer values have been obtained in several of my own studies. Likewise, the strength-duration curves obtained for stimulation of the skin by single pulses (Rollman 1969; 1975) are basically equivalent to those determined for single pulses in the visual cortex (Brindley 1973; Girvin, Evans, Dobelle, Mladejovcky, Henderson, Abramov, Gordon & Turkel 1979), while those for trains of electrocutaneous pulses match well the cortical data reported by Girvin et al. (1979), who found that phosphene thresholds decline rapidly and then level off as train duration is increased to about 180 msec.

The results presented above suggest, then, that movements toward a "harmonization of the central and peripheral theories of temporal summation" can come from direct psychophysical studies with humans as well as from intracellular investigations of the lateral eye of *Limulus*. Systematic control of electrocutaneous pulses offers the opportunity to assess behaviorally the response modes operating at a sensory system's periphery and center; as an added bonus, one can avoid the nonlinearities (Uttal 1979) that occur within the receptor. The human observer, with electrodes on the skin connected to a constant current stimulator, can provide an important preparation for psychophysicist and neurophysiologist alike.

Author's Response

Temporal summation and stimulus modality

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Rollman's thoughtful commentary on our target article (Wasserman & Kong 1979) appropriately distinguishes between our characterization of the literature on temporal summation and our attempt to formulate a chronometric theory from this characterization. Our literature characterization was founded on the notion that task-dependent differences in behavioral studies of temporal summation (i.e., energy-dependent versus time-dependent summation as well as critical duration variations) have their counterparts in coding-dependent variations in the properties of physiological responses. Every task-dependent behavioral variation did have a coding-dependent counterpart, suggesting that the sensory code was task dependent. We were able to offer a chronometric theory because the physiology provided information that one could not get from purely behavioral studies, namely an orderly relation between the critical duration of a neural response and that same response's latency. Hence we suggested that any behavioral critical duration would have to be associated with the latency of an unobservable response in the organism's nervous system. Thus behavioral critical durations could be a measure of mental timing.

Our analysis was based primarily on studies of temporal summation effects in visual physiology and perception. Rollman's commentary considers the case for nonvisual stimuli. He, however, really treats two different categories of nonvisual stimuli. On the one hand, he considers the use of natural sensory stimuli in nonvisual sense modalities. On the other hand, he considers the effects of electrical stimuli directly applied to the nervous system of a behaving organism. It will be useful to discuss these two different approaches separately, starting with the latter.

Correlational versus experimental approaches. Most studies of the neural mechanisms that mediate sensation and perception are intrinsically correlational in nature. In such studies, behavioral data patterns are correlated with the data patterns obtained from comparable physiological studies. Moreover, with some important exceptions, technical and economic limitations have usually made it necessary to correlate behavioral data obtained from human observers with physiological data derived from animal preparations. It is therefore possible, as we have indicated elsewhere (Wasserman & Kong 1974), for such correlations to be profoundly in error. It would be wrong, however, to conclude from the existence of such errors that we should abandon the correlational approach. It provides information that is often simply not obtainable by any other method. Many of the major organizing concepts of contemporary sensory science (e.g., lateral inhibition, feature detection, frequency-specific channels, spectral opponent mechanisms, etc.) were derived from correlational analyses. If we choose to abandon the correlational approach simply because it can sometimes lead us into error, we will be left with a mere skeleton of our present understanding of sensory systems. More important, to invoke the correlational criticism selectively when novel interpretations are offered would have a chilling effect on independent thought. Instead we have to recognize that the correlational approach will be with us in sensory science for a very long time (barring major technical breakthroughs) and that we will have to use it judiciously with full awareness of its limitations.

There is another approach, however, which, though it suffers from strong technical and ethical constraints, offers a powerful supplement to the correlational one. This alternative approach is intrinsically experimental in nature and completely avoids the species problem as well. It is the approach described in Rollman's commentary: one can (subject to certain technical and ethical constraints) directly influence the nervous system of a human observer with electrical stimulation. One can thereby directly manipulate the coding properties of afferent sensory signals and observe the effects of these coding variations on behavioral performance. If one found that a coding transformation produced a systematic transformation in behavior, then one would be on far more secure grounds in concluding that the putative code was a genuine sensory code. As Rollman points out, experimental work of this sort has been done in the somesthetic system, at both the peripheral and the cortical level. In addition, he notes that work has been carried out analyzing the visual sensations (phosphenes) evoked in blind patients by electrical stimulation of visual cortex. The greatest amount of work of this experimental sort has in fact been done with deaf patients who receive electrical stimulation via a prosthesis implanted in their cochlea. Elsewhere (Wasserman 1981) I have reviewed studies of these cochlear implants in detail. At the present time, more than 200 patients (House, Bode & Berliner 1981) are using such cochlear implants as artificial auditory receptors and deriving considerable benefit from them. Because the patent benefit of the cochlear implant provides a full ethical justification of the surgical risk, these patients constitute an enormous and largely untapped resource for sensory science, particularly for serious studies of sensory coding.

What have we learned from the experimental approach? Rollman nicely summarizes much of the information that he and others have obtained from such investigations. The general conclusion is quite consonant with the conclusion that Kong and I drew in our target article: The sensory code is task dependent because manipulations of the characteristics of artificially created sensory signals produce systematic manipulations in characteristics of the attendant sensations as a function of the observer's task. But there is more specific information available in this literature. One central proposition that emerged from our analysis of temporal summation was that there was a fundamental difference in the code used when detection was the task imposed on the subject and the code used when identification was the task. For detection, the behavioral response seemed to be mediated by the initial portion of the sensory signal, whereas for identification the behavior could only be quantitatively explained by assuming that it was

mediated by a far more extended sensory code. In fact, we found it necessary to integrate the entire receptor response in order to account for the behavior of an intact organism in our identification task.

Our interpretation was largely based on correlation evidence. Dobelle's group, working with a blind volunteer, has obtained experimental evidence directly corroborating this correlational conclusion. As Rollman notes, Girvin, Evans, Dobelle, Mladejovsky, Henderson, Abramov, Gordon, and Turkel (1979) found that the threshold for detecting a phosphene induced by stimulation of the visual cortex was only influenced by the duration of the cortical stimulus up to a duration somewhere between 100 and 200 msec. The task of the blind volunteer in the Girvin et al. experiment was only to report the presence or absence of a phosphene. The subject was not asked to report anything about the characteristics of the phosphene. However when he was asked to identify a characteristic of the phosphene (Evans, Gordon, Abramov, Mladejovksy & Dobelle 1979), the results were remarkably different, as shown in Figure 1. Here we plot the subject's identification of the brightness of the phosphene as a function of the cortical stimulus train duration. These identification data exhibit a pattern totally different from that of the detection data. There was in fact no limit to the contribution of the prosthetic signal to identification behavior up to 2½ seconds, which was the maximum duration used in this experiment. But above 200 msec, the same signal changes have no effect on the subject's ability to detect the presence or absence of the stimulus. The experimental results obtained by Evans et al. and Girvin et al. are just what we predicted in correlational analyses presented earlier in Wasserman, Felsten, and Easland (1978; 1979).

I therefore wish strongly to endorse Rollman's emphasis on the value of considering data obtained from an experimental approach to the sensory coding problem. Even though this approach is limited and can only be applied in certain specific situations, those situations in which it can be applied can give us powerful insights into the sensory coding problem.

Other sense modalities. Rollman also notes differences between the properties of temporal summation in the visual system and the properties of temporal summation in other sensory systems. According to Rollman, the critical duration in vision declines as stimulus intensity increases; in audition, however, it remains more or less invariant, whereas for warmth, the critical duration increases with the intensity of the stimulus. Let us assume for the moment that Rollman's characterization of the literature on this point is complete. What would be the implication of a genuine intersensory difference of this sort for either our characterization of the literature on temporal summation or our chronometric theory? There would in fact be little impact: Our chronometric analysis did not depend in any way on such trends; rather, it depended on an association between the critical duration of a neural response (whatever it was) and the latency of that same neural response. The treatment needed to produce covarying changes in both critical duration and latency would not matter for our chronometric theory although such information would
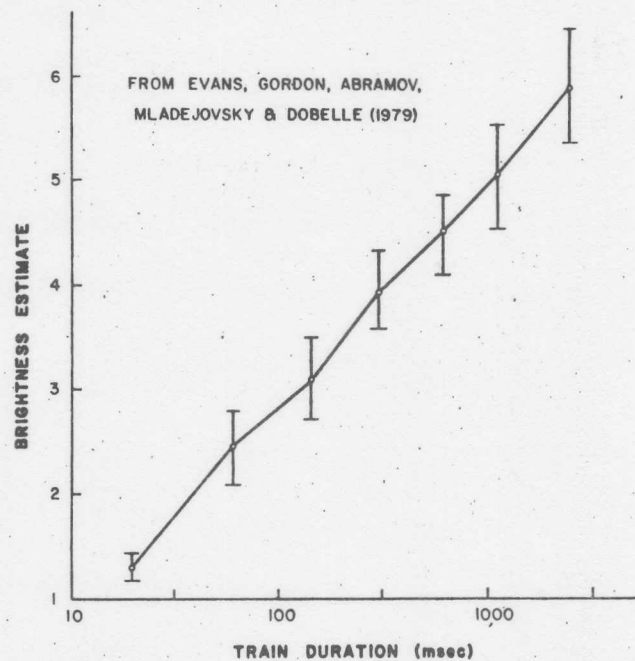

Figure 1 (Wasserman). Brightness identifications of phosphenes evoked by direct cortical stimulation with stimuli of various durations. This figure has been adapted from Figure 5 in Evans et al. (1979). Their figure gave brightness identification data separately for 10 different electrodes plotted against the number of pulses in the stimulus train. The data from those 10 electrodes have been averaged here. They have also been rescaled and are plotted here as a function of train duration. The error bars represent ±1 SE between electrodes. The rescaled and averaged results presented here are representative of the individual electrode results reported by Evans et al. in the sense that each individual electrode did give a function that was monotonically increasing. However each individual electrode's function was more irregular than the averaged and rescaled function. In the form given here, the data appear strikingly orderly and fall almost exactly on a straight line. Whether this orderliness is a genuine characteristic of these data or whether the irregularities present in the individual electrode data would be more representative cannot be determined with the data in hand. But whichever data presentation is used, it is clear that the behavior is influenced by increases in train duration of up to at least 2½ seconds.

be valuable for understanding the biophysical and biochemical bases of the summation effect itself. What would matter very much would be data that would tell us how the critical-duration/latency rule varied with variation among sense modalities. Thus, for a sense modality in which the critical duration increased with increasing intensity, what would be very germane to our hypothesis would be information on whether or not the latency of the same response also increased with increasing intensity. If this were not so, then our chronometric concepts would fail to be generalizable across sense modalities. But, as far as I can tell, none of this research bears on this point in any way. Hence the implications of this work for our chronometric theory are obscure.

However, intersensory comparisons are absolutely treacherous because it is so difficult to be certain that one is comparing comparable cases. In a single sense modality, many functional properties may depend upon

circumstances. For example, the right panel of Figure 2 of our target article showed that, under certain circumstances, the visual critical duration does decline with increasing intensity. But, as Figure 6 of our target article showed, there are also other circumstances in which the critical duration increases with increasing intensity. In order to compare vision with any other sense we have to decide how to compare the Figure 2 versus Figure 6 trends with comparable situations in a nonvisual sense. Even when we do decide that the circumstances are similar, we still have to worry about the fact that basic sensory variables can influence these trends. For example, we recently completed (Wang & Wasserman, unpublished data) a study of the effect of light adaptation on temporal summation in the *Limulus* photoreceptor. For four different features of the receptor response, we measured temporal summation in light and dark adaptation. For each of these four features, the range of variation of the critical duration in light adaptation was considerably smaller than it was for dark adaptation (even when every other aspect of the experiment was as comparable as we could make it). In fact, for one feature of the sensory response, the critical duration in light adaptation was virtually invariant with intensity.

Thus, for the sense modality with which I am most familiar, I can find data that show all three trends associated by Rollman with intersensory differences. In order to make a comparison across sense modalities, one really needs a conceptual framework within which one can plausibly assert that the measurements have truly been made under comparable conditions. This is an extremely difficult thing to do. Consider, for example, the Stevens and Hall (1966) investigation wherein temporal summation was studied in vision and audition under what one would have hoped would be quite comparable circumstances. Radical differences in procedure unfortunately guaranteed that the results would not be commensurable between the two sense modalities. Recall that adaptation is an important variable affecting the dependence of critical duration on intensity.

The adaptation state of the Stevens and Hall subjects was clearly different when they were being asked to judge visual stimuli from what it was when they were being asked to judge auditory stimuli. In the case of the visual stimuli, flashes of light were presented with a 15-second interstimulus interval. But in the auditory case, noise bursts were delivered at 0.9-second interstimulus intervals. Under these particular circumstances Stevens and Hall found that the visual critical duration declined substantially as the intensity was raised whereas the auditory critical duration remained largely invariant. But suppose the experiment had been done with the interstimulus intervals reversed, using a 0.9-second interval in vision and a 15-second interval in audition. There is absolutely no doubt that the results would have been substantially influenced by such a manipulation. The visual system would have been very strongly light adapted. Our data, as well as many other data, indicate that the visual critical durations would thereby vary over a much narrower range, and perhaps they would not vary at all. In the auditory case, there can be little doubt that an increase in the interstimulus interval would have reduced the adapting effect of one stimulus on the perception of the next.

I am unaware of any data in audition that describes the effect of adaptation on the critical duration. But there are data from both Miller (1948) and Small, Brandt, and Cox (1962) that show that, at least under some circumstances, the auditory critical duration does decline with increasing intensity. In fact, the data of Small et al. show that a 50-dB increase in stimulus intensity reduces the critical duration from 50 msec to 15 msec, which is a more than threefold change. There can be little doubt that an experiment could have been designed in which the direction and magnitude of the intensity-dependent changes in the critical duration in the two sense modalities would have been identical. One could reach no conclusion about the relative characteristics of the various sense modalities from any such single experiment, however, unless one had some strong basis for saying that the conditions of the experiment were truly comparable. And any such experimental tour de force would still not bear on the central issue raised in our target article, namely the orderly relation between the critical duration of a neural response and its latency, which permits one to infer the latency from the critical duration.

The critical-duration/latency rule. Our chronometric theory was built on the rule that we found in the dark-adapted *Limulus* photoreceptor, namely that the critical duration was equal to the latency minus 66 msec. In both our target article (Wasserman & Kong 1979, p. 249) and the response to the initial commentaries (Wasserman 1979, p. 299) we indicated that the robustness of this rule and its generality in situations and species other than the one we investigated were of cardinal importance in determining the applicability of our chronometric theory. Rollman's commentary does not address this issue. But we would like to take this opportunity to provide our colleagues with a brief indication of the nature of some recent data we have collected on the robustness question.

We studied the critical-duration/latency rule in the *Limulus* photoreceptor in both dark and light adaptation (Wang and Wasserman, unpublished data). The dark-adapted state was more dark adapted than the moderately dark-adapted state used by Kong and Wasserman (1978), while the light-adapted state was substantially more light adapted. Wang and Wasserman found that under dark adaptation the critical duration equaled the latency minus 33 msec whereas under light adaptation (all other factors being as equal as we could make them) the critical duration equaled 0.56 times the latency.

These three investigations suggest that adaptation has an orderly effect on the critical-duration/latency relation. The more dark adapted the visual system, the closer the relation approaches the tautologic limit described by Hartline (1934), namely that the critical duration of a response cannot be longer than its latency. Hence the Hartline limit is that the critical duration is equal to the latency. As the visual system is progressively more light adapted, the critical-duration/latency relation progressively moves away from the Hartline limit. Then, as light adaptation proceeds still further, the relation tilts over and flattens out. Thus, instead of a single critical-duration/latency rule, it appears that a fan of rules exists which has an orderly dependence on the state of adaptation.

This finding indicates that the utility of the critical duration as a chronometric indicator of mental activities will depend on a serious attempt to control the state of adaptation during any behavioral experiment. But the fact that an orderly rule exists in every state of adaptation yet studied indicates that the basic chronometric principle is robust.

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