Perceived duration, visual persistence, and neural integration

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Varying stimulus intensity while measuring the perceived duration/visual persistence of brief light flashes has yielded disparate results. Some studies have found a direct relationship between the two variables; others have found an inverse relationship. Several models have been suggested to unify this behavioral literature. They invoke the absolute intensity and the nature of the judgment as explanatory variables. We now present physiological data whose analysis was motivated by these models. We measured the duration of photoreceptor potentials as a function of light intensity and response measure. One response measure was the length of time required for the response to decline from the peak by a criterion amount. The other response measure was the length of time a response stayed above a criterion level. These data suggest that each behaviorally based model captured a different aspect of a single underlying mechanism and that a melding of the two critical concepts would harmonize all of the results: In this melding, the sensory signals that mediate visual perception would have the type of complex intensity- and time-dependent properties found in real neural responses.

Visual sensations need not last for the same amount of time as the light flashes that evoke them. If, as is often the case, the sensation outlasts the stimulus, then one can talk about visual persistence: the length of time between the end of the stimulus and the end of the sensation. Alternatively, one can talk about perceived duration; it is usually operationally defined as the time from stimulus onset to the end of the sensation. Sometimes, however, perceived duration is defined as the interval between the beginning and end of the sensation. Whichever measure is used, differences between objective and subjective duration are particularly interesting for two reasons: First, they are quite obviously expressions of the mechanisms that create subjective representations of the external world. Second, they also provide particularly tractable material for quantitative empirical investigation. A large number of studies have therefore measured the effects of stimulus intensity on visual persistence and perceived duration; the results of these studies have not been uniform. Some of these studies have found a direct relationship, whereas other studies have found an inverse relationship.

Several hypotheses have been offered to explain these variant results (see Coltheart, 1980; DiLollo, 1984; Hawkins & Shulman, 1979; Long, 1979, 1980, 1985). A more extensive review of these theoretical papers and the data on which they draw has been given elsewhere

(Nisly, 1985). Two principal alternative explanations exist. One explanation was formulated by Hawkins and Shulman and by Long; it suggests that an additional variable interacts with stimulus intensity to produce the divergence in the results. The implicated variable is the nature of the judgment required of subjects. On this hypothesis, some studies asked subjects to indicate when they first saw an offset (or decrease) in the magnitude of their sensation. Other studies asked them to indicate when they no longer had any visual sensation at all. Long and Gildea (1981) further clarified the difference between judgments by suggesting that an experimental paradigm that called for a sensation-offset judgment was not really a study of persistence at all, as it had traditionally been defined, because such a paradigm did not try to measure the entire sensory residual. By contrast, the complementary judgment measured the entire sensory signal and thus, by definition, was a measure of the sum of visual persistence. Thus, one judgment can be referred to as a judgment of *sensation offset*, and the other judgment can be referred to as a judgment of *total persistence*.

A second explanation was formulated by Coltheart (1980) and explored by DiLollo (1984); it suggested that stimulus intensity itself was the critical variable. On this hypothesis, responses evoked by intensities below an index intensity should yield an inverse relationship, whereas responses evoked by intensities above that index should yield a direct relationship.

These competing explanations have been assessed mainly by extensive analyses of the behavioral literature. Studies have been organized into categories according to experimental paradigm and instructional set (DiLollo, 1984; Long, 1979, 1980, 1985; Nisly, 1985). In addition, certain explicit experimental tests have been executed

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(see Long & McCarthy, 1982). Some investigators have implicated other variables, such as the distinction between the persistence of a sensory representation and the persistence of the abstract information resident in the representation (see Coltheart, 1980).

The present paper considers an essential conceptual ingredient implicated in these competing explanations, namely the waveform of the sensory signal that represents a light flash. Sometimes this waveform has been an explicit ingredient of the discussion, as in the hypothetical exponentially declining waveforms depicted by Hawkins and Shulman (1979) in their Figure 1. More typically, these signals and their waveforms have had a more tacit treatment.

An alternative approach to the signal waveform question comes from the suggestion that there is a relationship between behavior and activity in the nervous system. On that suggestion, well-founded models derived from behavioral studies of perceived duration would be sensitive to data on the physiological relationship between stimulus intensity and response duration. Such models would then have a particular interest in the waveforms of real sensory signals.

Real sensory signals are, of course, neural potentials that come in a variety of forms with certain common properties. In receptors and postsynaptic regions, neural signals come in the form of slow potentials that vary in amplitude. In axons, neural signals come in the form of brief impulses that vary in frequency. Both forms can be represented in comparable ways for analysis: Receptor and synaptic potentials can be viewed as plots of voltage as a function of time. Impulses can be viewed as plots of frequency as a function of time. Both signals generally respond to a transient stimulus by rising to a peak (or sagging to a trough) and then returning closer to baseline.

These neural responses change as intensity changes. When stimulus intensity is increased, the size of the peak response increases, latency decreases, and the response also rises more rapidly to the peak. For short durations, varying stimulus duration affects neural responses in a similar manner. But longer stimuli may evoke a sustained plateau, which then returns to baseline after flash offset.

In contrast to the extensive interest of psychophysical researchers in the question of perceived duration, little physiological research has explicitly addressed the question of response duration. Only a few relevant studies therefore exist.

One was done by Felsten and Wasserman (1981), who varied stimulus duration while holding intensity constant. They measured the effect of this treatment on duration of the receptor potential. They asked whether the neural waveform could reproduce the pattern of results that had been reported in a behavioral study by Haber and Standing (1970). A particular feature of the receptor waveform indeed gave neural results that quantitatively corresponded to the behavioral measures of perceived duration. This feature was how long the response stayed above a crite-

rium potential. It closely resembles the psychophysical total-persistence measure of the Hawkins and Shulman (1979) model and of Long's (1979, 1985) analysis.

In another relevant experiment, Duysens, Orban, Cremieux, and Maes (1985) recorded responses of cortical cells in the cat as a function of changes in stimulus duration. They distinguished between two kinds of cortical cells: cells with off and on receptive-field subregions that overlapped and cells with subregions that did not overlap. They also used high- and medium-light contrast levels (which was effectively the same as using different adaptation states).

When cells with overlapping off and on subregions were stimulated, there were no clear differences in response pattern as a function of stimulus duration for any contrast level. A more definite trend, however, existed in those cells that had nonoverlapping subregions. In the medium-contrast state, persistence after stimulus offset could be found to increase both in duration and amplitude as stimulus duration decreased. In the high-contrast state, this inverse duration effect could not be demonstrated.

Duysens et al. (1985) did not measure persistence quantitatively; they did discuss it qualitatively by referring to the form of their responses. When a waveform is a simple monotonic function that declines smoothly after the peak, a qualitative analysis can be straightforward. Most of these responses, however, did not return to baseline in such a simple manner; there were many oscillations in the responses. When such oscillations occur, it is not clear how one measures persistence: When several peaks occur, which one is important? How is decline to be measured? Is it the first decline or a later decline, or a combination of more than one decline? The primary implication one draws from this qualitative investigation is that central studies require more explicit rules for assessing how persistence is represented at this level of the nervous system.

Missing from this literature is reliable quantitative information on the way the duration of real sensory signals varies as intensity is varied. Hypothetical sensory signals have been invoked by behavioral investigators, but they are clearly model-dependent concepts. Physiological data do exist, but they have often been presented only in a phenomenological sense. Rarely have coding issues been considered. We therefore executed a study that attempted to address these issues directly. We analyzed receptor potentials for two reasons: (1) Virtually all receptors, regardless of species, yield potentials that have the same general waveform. (Photoreceptors taken from vertebrates usually give hyperpolarizing receptor potentials, whereas those taken from invertebrates usually give depolarizing receptor potentials. This inversion in the sign of the response is understood to be a trivial difference with regard to coding, since the polarity of the sensory signal can be [and often is] reversed by synaptic inhibition.) (2) The receptor potential waveform is relatively simple in shape. Thus,

the receptor provides a point of initial analysis that offers the hope of obtaining tractable results that are likely to be generally valid without requiring the postulation of the kinds of psychobiological combination rules that are necessary at more central neural levels after divergence and convergence have produced parallel processors.

One aim of our experiment was to measure the effect of intensity on real neural potentials when persistence is characterized by the absence of a sensory residue. A way to determine this effect would be to vary light intensity and then measure the time that the neural response stays above a criterion level. If this neural measure had any relation to behavioral judgments of total persistence, one would expect a direct trend.

A second aim was to learn about response offsets in the visual system. No earlier work had been done on any possible sensory codes that might underlie this judgment. The judgment-dependent model, however, would suggest that sensation offset should be related to the decline of the response after the peak. One way to examine this concept would be to choose a criterion response drop and measure how such a decline varies as intensity is varied. If this measure of neural-response offset indeed had some relation to the judgments of sensation offset that had been characterized in the behavioral literature, then one would predict a negative relationship between intensity and the time for the response to drop a criterion amount from the peak.

Serious problems occur if one fails to distinguish clearly between physiological and behavioral measurements. An investigation of the present sort can only provide information about the characteristics of potential sensory codes; it cannot establish their validity by itself. It is therefore critical to use different names for the measures in the two domains. One physiological measure will therefore be called the *end code*. It will be taken as the time that the receptor potential stays above a criterion level. It is postulated to be comparable to behavioral measures of total persistence. The other physiological measure will be called the *drop code*. It will be determined by the time when the receptor potential drops from the peak by a criterion amount. This code is therefore postulated to be related to behavioral judgments of sensation offset.

METHOD

Intracellular recordings were taken from the photoreceptors of the lateral eye of *Limulus*. The methods used in data collection were quite conventional and have been described elsewhere (Wang & Wasserman, 1985). An important aspect of this work is that adaptation was strictly controlled by continuous positive measurements of the state of adaptation that were taken throughout the experiment.

The end-code measure was how long a neural waveform stayed above a given criterion. Figure 1 illustrates how this measurement was made on a representative photoreceptor potential at one particular criterion level.

The drop-code measure of interest was how long it took for the receptor potential to drop by a criterion amount from its peak. This

Figure 1. The method used to make end-code measurements: A given criterion level was chosen first, and then the length of time that the response waveform stayed above that chosen criterion level was calculated. The waveform in this figure is a plot of a photoreceptor potential as a function of time. It is 10 sec long. It contains a 10-mV calibration marker that was inserted at the beginning of the trace before the light flash was delivered. The shortest stimulus duration used (20 msec) would last about the length of time that would be represented by a line slightly thinner than those used in this figure. The longest stimulus duration used (160 msec) would be slightly shorter than the length of time represented by the calibration marker.

was done by choosing a particular criterion and measuring how long it took for the response to drop down by that amount. This measurement process is illustrated in Figure 2 for the identical receptor potential.

For both measures, 20 criteria, which covered the entire possible physiological range of the responses (namely from 5 to 100 mV) in increments of 5 mV, were chosen. A total of four different parameters were therefore manipulated: adaptation state, stimulus intensity, criterion level, and type of analysis.

RESULTS

The data are in the form of parametric plots of the effect of stimulus intensity on response duration. The value of the criterion is a parameter that varies within every such plot. The adaptation and sensory code parameters vary between plots.

End Code

The end-code results for a typical cell are shown in Figures 3 and 4. Light-adapted data are shown in Figure 3, and dark-adapted data are shown in Figure 4. The result is clear: Regardless of state of adaptation or criterion, a direct monotonic relationship generally exists between intensity and response duration.

There is, of course, a systematic effect of criterion on response duration. Lower criteria yield longer response

Figure 2. The method used to make drop-code measurements: A given criterion was chosen first, and then the length of time between stimulus onset and the time when the response waveform decayed to that criterion was calculated. The waveform is identical to the one in Figure 1.

durations. But the curves are not parallel. The responses at the lower criteria were more dramatically affected by changes in intensity than were the responses at higher criteria.

Drop Code

The drop-code results for the same cell are shown in Figures 5 and 6. Light-adapted data are shown in Figure 5, and dark-adapted data are shown in Figure 6. Regardless of state of adaptation or criterion level, an inverse relationship generally exists between stimulus intensity and response duration for low stimulus intensities, and a direct relationship exists at high intensities. Overall, a U-shaped relation exists between the response duration and intensity.

There is a systematic effect of criterion on response duration. The lower criteria yielded shorter responses than did the higher, and there was a systematic change in response from one criterion to the next.

Adaptation and Sensitivity

It is known, almost by definition, that light adaptation reduces visual sensitivity. In the present case, quantitative measures of visual sensitivity are readily available in the form of the semisaturating constants (σ) of the Naka-Rushton (1966) equation ($V/V_{\max} = I/I + \sigma$) where V is the peak response, $V_{\max}$ is the saturating value of the peak

response, and I is light intensity. The value of σ is marked by an arrowhead on the intensity axes of Figures 3-6. This indicates the intensity that produced a response that is half of the maximum (or saturating) response. In log attenuation units, σ was 5.3 in the dark-adapted state and 4.0 in the light-adapted state (see Wang & Wasserman, 1985). Hence, the change in sensitivity was 1.3 log units, or 20-fold.

These values of σ permit one to ask whether the effect of light adaptation on response duration can be accounted for simply by appealing to a sensitivity shift. The response-duration plots will superimpose quite well if the shift suggested by the Naka-Rushton sensitivity measure is made. Such a superimposition is particularly effective in aligning the inflections in the end-code data and the minima of the U-shaped function for the drop-code data.

DISCUSSION

The primary finding of this experiment is that adaptation, intensity, and type of measurement were all effective variables.

Effect of Adaptation

Light adaptation produced sensitivity differences that could be compensated by appropriate intensity adjustments. This suggests that, at least over the range of values

Figure 3. Effect of intensity (expressed in log attenuation units relative to 250 W/m^2) on response duration (measured in seconds) when end-code measurements were made in a light-adapted state. Each curve represents data yielded by a different criterion. The values of alternate criteria are indicated in millivolts; intermediate criteria are not labeled, but these fell at 5-mV intervals. The value of σ represents the intensity that produced, for this particular cell (No. 17), a response that was half of the maximum or saturating response. See text for a complete explanation of σ .

Figure 4. Effect of intensity on response duration when end-code measurements were made on cell No. 17 in a dark-adapted state. Figure composed in the same manner as Figure 3.

tested, the major effect of light adaptation on response duration is mediated by its effect on sensitivity. It also demonstrates the critical importance of accounting for adaptive state in any study of perceived duration. Much of the variance between studies may be caused by differences in adaptive state.

This finding also implies that if our dark-adapted data had been extended to yet lower intensities, they would have yielded an even more dramatic U-shaped relationship than was found with the intensities actually used in this experiment.

Characterization of the Principal Findings of this Study

Given that a consistent set of results emerges when one allows for the effect of adaptation, what do these results imply about the duration of sensory responses?

End Code

The effect of intensity on end-coded responses is to increase response duration as stimulus intensity increases. But the rate of change was not constant; the slope of the curves was flatter for lower intensities than for higher intensities. Nonetheless, the result is consistent with the hypothesis that behavioral response duration measured by total persistence is related to the end-code measure of neural persistence. And similar slope changes are evident in the behavioral data as well.

Drop Code

A U-shaped relationship was found between the drop-coded measure of response duration and stimulus intensity, with a clear minimum of about 2.4 log attenuation units in the light-adapted case. This finding is apparently

Figure 5. Effect of intensity on response duration when drop-code measurements were made on cell No. 17 in a light-adapted state. Figure composed in the same manner as Figure 3.

unique; no other study of the duration of visual responses, behavioral or physiological, has previously reported such a trend. To interpret this result, it is necessary to fix the U-shaped trend in an appropriate metrical context: The intensities in the present physiological experiments covered an irradiance range of 5.4 log units. The maximum unattenuated irradiance was 250 W/m^2 , which is 2.4 log W/m^2 or 5.4 log mW/m^2 . The behavioral data mostly cover a luminance range that extends from about -2 to 3 log cd/m^2 (cf. the more complete metrical analysis given

Figure 6. Effect of intensity on response duration when drop-code measurements were made on cell No. 17 in a dark-adapted state. Figure composed in the same manner as Figure 3.

in Nisly, 1985). The only sensation-offset study that used very high intensities (which extended up to about 5 log cd/m²) was one done by Pease and Sticht (1965).

It is difficult to make an exact comparison of the physiological irradiance units and the behavioral luminance units without knowing the spectra and geometry of the various stimuli. We estimated the order of magnitude of this conversion by measuring the irradiance on and the luminance of identical broadband stimuli. We did not attempt to assess the differential effects of ocular transmission and collection factors. This rough conversion indicated that the two scales for irradiance (in mW/m²) and luminance (in cd/m²) would have similar numerical values. Using this as a guide suggests that most of the behavioral data generally have been taken at lower intensities than the present physiological data.

This calibration then divides the analysis into lower versus higher intensities. With the exception of the Pease and Sticht (1965) study, the behavioral studies had a maximum intensity of about 3 log cd/m², which would roughly correspond to about 3 log mW/m², or 2.4 log attenuation units, which would fall at the minimum of the light-adapted U-shaped function. So the physiological data also roughly divide at this intensity.

Lower Intensities. The sensation-offset behavioral data and the drop-code data from corresponding intensities both yielded a negative relationship between intensity and the independent variable at these intensities. This good agreement between physiology and behavior would reinforce the hypothesis that sensation offset judgments were related to response drops if one's attention was restricted to lower intensities.

Higher Intensities. To our knowledge, there is only one behavioral study of sensation offset that manipulated intensities as high as those used in the physiological drop-code study, namely, the study done by Pease and Sticht (1965). They used reaction time as their response measure. Their stimuli covered a range from 0.8 to 5.0 log cd/m². Adaptation was not strictly controlled, and therefore the effectiveness of their highest intensity stimuli was reduced to an unknown degree. If the drop code is a valid correlate of the sensation-offset judgment, and if reaction time is a fair response measure, one would predict a U-shaped relation between intensity and reaction time for these higher intensities. The data obtained by Pease and Sticht are not inconsistent with this notion, although a clear and symmetrical U-shaped function is not present in their data. Instead, their data all follow a reversed-J-shaped pattern, with the data declining at lower intensities and then leveling off at higher intensities. Some of their data actually turn up slightly at the highest intensities, forming an asymmetrical U-shaped function. This strong prediction therefore needs to be tested further. It would be desirable to collect more behavioral data in the highest range of intensities, using a method that measures sensation offset. In such a critical study, strict control of adaptation would be essential.

Utility of the Proposed Models

Different models have been proposed to explain the discrepant results of behavioral studies of perceived duration. Each has been previously evaluated in terms of its ability to account for the behavioral data. The models can now be evaluated in relation to the present physiological data.

The Judgment-Dependence Model

The judgment-dependence model asserts that the diverse trends found in the behavioral literature can best be differentiated in terms of the nature of the judgment required of the subject. The differentiation between sensation-offset and total-persistence judgments suggested corresponding physiological codes. Specifically, the sensation-offset judgment should be related to the drop-code measure and the total-persistence judgment should be related to the end-code measure. This characterization of the judgment-dependence model, as it currently stands, is congruent with most of the trends in the physiological data but not with that in the higher intensity drop-code data.

If the physiological drop code does actually correspond to the behavioral sensation-offset judgment, then the judgment-dependence model would need to be modified by an alteration in its fundamental assumption about the waveforms of sensory signals. In its most specific form, it assumed they were declining exponentials. But real sensory signals are certainly more complex than that, and the present results suggest that this assumption may need modification.

The Intensity-Dependence Model

Coltheart (1980) and DiLollo (1984) suggested that a more appropriate way to categorize the perceived duration data would be to divide them by stimulus intensity. They suggested that at intensities below a certain level, namely about 2.3 log cd/m², intensity and perceived duration were negatively related, but that at intensities above 2.3 log cd/m² a positive relationship is found between these two variables. This would be a U-shaped trend; it would be similar in form to the U-shaped trend found in the present study. Moreover, its minimum falls at roughly the intensity that yielded our minima. If the U-shaped trend had been our only finding, then the intensity-dependence model would have been very strongly supported. However, since changing the measure changes the trend, this leaves the theory in a more problematic state. An outcome of the present investigation that is particularly relevant for intensity-dependent models is that intensity per se should not be of principal importance; instead, intensity relative to adaptation level should carry the burden.

Summary

Neither of the models, as each currently stands, is fully able to account for all of the data. Each model predicted

a portion of the present results: The judgment model predicted that different analyses of identical sensory signals would make a difference. They did. The intensity model predicted that the trend itself would be intensity-dependent. It was.

The data suggest that all of the results may be harmonized by a complex melding of the two approaches: The judgment-dependent model would be able to account for both the physiological and the behavioral perceived-duration results if it incorporated an intensity-dependent property, namely the complex intensity dependence of the waveform of real sensory signals. A more successful model would merely need to incorporate the judgment distinction with the postulation that the sensory signals that govern behavior actually have intensity-dependent waveforms of the type exhibited by real sensory neurons. A very strong test of this hypothesis is available: It predicts a symmetrical U-shaped result when sensation-offset judgments are made over a wide enough range of intensities with strict control of the state of adaptation.

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