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Inverse-Intensity Effect in Duration of Visible Persistence

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Duration of visible persistence can vary inversely with stimulus intensity. This inverse-intensity effect is obtained by varying the intensity of the stimuli or of the background, provided that the variations extend into the mesopic range. A similar relationship—known as the Ferry-Porter law—holds for the critical frequency at fusion (CFF). The authors propose that studies of CFF, 2-pulse threshold, and visible persistence can be encompassed within 1 conceptual framework in which the effect is modeled by the progressive reduction in the temporal extent of the positive phase of the system's response as the level of light adaptation changes from scotopic to photopic. In this context, the authors present an integrative scheme in which G. Sperling and M. M. Sondhi's (1968) formal model and M. Coltheart's (1980) neurophysiological conjecture are shown to be compatible and complementary accounts of the effect.

It has been known for some time that the sensation produced by a brief visual stimulus can outlast the duration of the external display. An example of this illusion can be seen occasionally around campfires: A burning ember at the end of a stick spun through the air is seen as an arc of light whose length varies with velocity. According to Plateau (1829; cited in Boynton, 1972), the prolonged visibility of brief stimuli was known to Aristotle in the third century B.C. In more recent times, Coltheart (1980) termed this phenomenon *visible persistence.*

Some Determining Factors

Visible persistence has been studied extensively since the publication of Sperling's (1960) monograph on iconic memory. In a comprehensive review of the literature, Coltheart (1980) listed over 130 pertinent titles; more have appeared since. In the main, these studies were aimed at estimating the duration of visible persistence and at identifying the major underlying variables. Duration of visible persistence was found to be related *inversely* to three stimulus variables: (a) duration of the stimulus (e.g., Di Lollo, 1980; Efron, 1970), (b) spatial proximity of successively presented stimuli (e.g., Di Lollo & Hogben, 1985; Farrell, 1984), and (c) intensity of the stimuli (e.g., Allport, 1968; Castet, Lorenceau, & Bonnet, 1993). These have come to be known as the *inverse-duration effect,* the *inverse-proximity effect,* and the *inverse-intensity effect,* respectively.

Each of these effects has been documented by ample empirical evidence. However, the evidence is not uniform. To our knowledge, there have been few—if any—failures to obtain either the inverse-duration or the inverse-proximity effect. By contrast, there have been several studies in which an inverse-intensity effect failed to materialize. As a first step in exploring this variability, we compared some studies in which the inverse-intensity effect had been found with studies in which it had not been found. The comparison, however, did not reveal any single factor—such as type of stimuli or experimental paradigm—that could account for the different outcomes. We also considered the possibility that the effect of intensity on persistence may be invariably weak and hence that the effect might become hidden in experimental noise. This cannot always be true, however, because the inverse-intensity effect can be quite large: In a study by Allport (1968), it accounted for over 25% of the total duration of visible persistence.

Despite the variability in outcomes, the inverse-intensity effect cannot be regarded as theoretically unimportant or of limited scope: Coltheart (1980) showed that it plays a crucial role in distinguishing between various aspects of iconic memory. As we show below, the effect is also closely linked to the classical Ferry-Porter law, which formalized the inverse-intensity effect found in studies of critical frequency at fusion (CFF). In view of its potential importance and generality, we set out to identify the variables that underlie the inverse-intensity effect in any given study. To this end, we searched the experimental literature for variables that covaried with a presence or absence of the effect. Our survey revealed that, in any given study, occurrence of the effect depends jointly on the absolute intensity levels and the range of stimulus and background intensities used. We then summarize the empirical evidence and present a hypothesis capable of accounting for the bulk of the studies in which the effect was found and for instances in which it was not found.

Procedural Background

Most estimates of visible persistence are based on perceived temporal continuity of sequential stimuli displayed in different

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spatial locations. Successive stimuli are usually separated by a temporal gap (the interstimulus interval, or ISI). At very short ISIs, successive stimuli are perceived as temporally contiguous or overlapping. This overlap occurs when the duration of visible persistence exceeds the duration of ISI. Estimates of the duration of visible persistence are obtained by increasing ISI until sequential stimuli are no longer seen as temporally overlapping.

In practice, perceived temporal contiguity has been assessed in several ways: Efron's (1970) observers adjusted the onset of a trailing stimulus until it coincided with the perceived termination of a leading stimulus; Farrell, Pavel, and Sperling's (1990) observers adjusted ISI between sequential stimuli until all stimuli in the series appeared to be subjectively present at the same time; and Eriksen and Collins (1967) required observers to identify a configuration that emerged from the temporal integration of two sequential images, each containing meaningless features when viewed in isolation.

Manipulating the intensity of the displays often (though by no means always) produces an inverse-intensity effect: The estimated duration of visible persistence decreases as the intensity of the display is increased. The effect is obtained whether changes are made in the intensity of the background or of the stimuli themselves. Inverse-intensity effects have been obtained by varying the intensity of the stimuli on a background of fixed luminance (Allport, 1968; Efron & Lee, 1971; Di Lollo & Hogben, 1987) or by varying the intensity of the background on which the stimuli are presented (Dixon & Hammond, 1972; Hogben & Di Lollo, 1985).

Empirical Evidence for the Inverse-Intensity Effect

In reviewing the evidence for the effect of intensity on visible persistence, we proceed as follows. First, we consider experiments in which stimuli of varying intensity were displayed on backgrounds of fixed luminance. Next, we deal with experiments in which the background was varied. In each case, we distinguish studies in which an inverse-intensity effect was obtained from those in which the intensity of stimulation had no significant effect on performance. Finally, we examine studies in which direct-intensity effects were found.

Varied Stimuli, Fixed Background

Summarized in Table 1 are experiments in which stimuli of different intensities were displayed on backgrounds of fixed luminance. Listed in the upper portion of Table 1 are studies in which an inverse-intensity effect was found; listed in the lower portion are studies in which the stimulus intensity had no effect on performance.

We postpone a discussion of the data in Table 1 until the evidence in Table 2 has been presented. It is of interest to note a general trend regarding luminance levels of stimuli and back-

Table 1
Inverse-Intensity Effect: Stimuli of Varying Intensity on Fixed Background

Author	Background (log cd/m^2)	Stimuli (log cd/m^2)	Task
		Inverse-intensity effect found	
Allport (1968)	−1.52	1.43 1.74 2.24 2.54	Phenomenal simultaneity or continuity
Allport (1970, Exp. 1)	dark	0.23 1.54	Phenomenal simultaneity or continuity
Allport (1970, Exp. 2)	dark	0.23 0.71 1.23 1.93	Phenomenal simultaneity or continuity
Bartlett et al. (1968)	dark	−1.39 0.39 0.61 (red)	Onset–offset reaction time
Bartlett et al. (1968)	dark	−1.85 0.86 0.14 (blue)	Onset–offset reaction time
Bowen et al. (1974, Exp. 1)	dark	0.04 0.99	Synchrony judgments (target–probe)
Bowen et al. (1974, Exp. 2)	dark	−0.05 0.99	Synchrony judgments (target–probe)
R.H. Brown (1958)	dark	0.2–4.5	Loss of motion perception
Castet et al. (1993, Exp. 1)	−0.44	0.79 1.05 1.56	Phenomenal simultaneity or continuity
Di Lollo et al. (1988, Exp. 3)	dark	−0.20 0.95	Temporal integration of form parts
Di Lollo & Hogben (1987)	−0.52	1 or 2 L.U. above threshold	Temporal integration of form parts
Dixon & Hammond (1972)	dark	bright or dim	Phenomenal simultaneity or continuity
Efron (1970, Exp. 3)	dark	−0.70 0.08 0.53 1.06	Synchrony judgments (target–probe)
Efron & Lee (1971)	dim	−0.89 0.61	Phenomenal simultaneity or continuity
Pease & Sticht (1965)	dark	0.8 1.0 3.0 5.0	Onset–offset reaction time
Sakitt & Long (1979)	−2.02	0.54 0.86 1.17 1.27	Synchrony judgments (target–probe)
Smith (1969)	dark	−0.5 0.5 1.5 2.5 3.5	Loss of motion perception
		Inverse-intensity effect not found	
Adelson & Jonides (1980, Exp. 1)	1.46	1.44 1.75 2.05 2.35	Partial report
Adelson & Jonides (1980, Exp. 2a)	1.90	1.50 2.20	Partial report
Adelson & Jonides (1980, Exp. 2b)	2.38	1.50 2.20	Partial report
Di Lollo & Bourassa (1983, Exp. 3)	0.95	0.8 to 2.1 L.U. above threshold	Temporal integration of form parts
Farrell et al. (1990)	−0.46	2.38 2.69 3.02	Phenomenal simultaneity or continuity
Hogben & Di Lollo (1985)	−0.52 0.48 1.48	1 L.U. below max to max	Phenomenal simultaneity or continuity
Wilson (1983)	1.08	1.42 2.13	Temporal integration of form parts

Note. Exp. Experiment; L.U. = log unit; max = maximum.

Table 2
Inverse-Intensity Effect: Stimuli of Fixed Intensity on Varying Background

Author	Background (log cd/m^2)	Stimuli (log cd/m^2)	Task
Inverse-intensity effect found			
Allport (1970, Exp. 3)	−2.00 −0.89 0.11 1.11 2.11	strobe	Phenomenal simultaneity or continuity
Castet et al. (1993, Exp. 2)	−0.44 −0.12	dep. var.	Phenomenal simultaneity or continuity
Dixon & Hammond (1972)	−1.15 0.85	bright or dim	Phenomenal simultaneity or continuity
Haber & Standing (1969)	0.2 2.2	black ring	Phenomenal simultaneity or continuity
Hogben & Di Lollo (1985)	−0.52 0.48 1.48	1 L.U. below max, to max	Phenomenal simultaneity or continuity
Long (1985)	−0.50 0.48 1.48	0–3	Synchrony judgments (target–probe)
Long & Beaton (1982, Exp. 2)	−0.52 0.53 1.53 2.01	0.53 1.01 1.71 2.01	Partial report
Long & Gildea (1981)	0.53 1.23 1.54	1.23	Synchrony judgments (target–probe)
Long & McCarthy (1982a)	1.23 1.71	1.23	Synchrony judgments (target–probe)
Long & Sakitt (1981)	0.23 1.23 2.23	as background	Phenomenal simultaneity or continuity
Inverse-intensity effect not found			
Adelson & Jonides (1980, Exp. 2a)	1.90 2.38	1.50	Partial report
Adelson & Jonides (1980, Exp. 2b)	1.90 2.38	2.20	Partial report

Note. dep. var. = dependent variable; Exp. = Experiment; L.U. = log unit; max = maximum.

grounds. With some exceptions discussed below, studies in which an inverse-intensity effect was found used backgrounds that were dim or dark and stimulus luminances that extended from low-mesopic or scotopic levels to higher values. By contrast, studies in which the effect failed to appear used relatively bright backgrounds and did not include low-luminance stimuli.

Fixed Stimuli, Varied Background

Listed in Table 2 are studies in which duration of visible persistence was estimated as a function of the intensity of the background field. Included are studies in which stimuli of fixed intensity were displayed on fields of different intensities and studies in which the space-average luminance of the entire display field was varied.

The data in Table 2 reveal much the same trend as the data in Table 1 regarding the effect of luminance levels. In general, the range of background intensities in the studies that found an inverse-intensity effect extended from low-mesopic or scotopic levels to higher values. This was not true, however, for the only study in Table 2 that failed to find an effect of background intensity (Adelson & Jonides, 1980).

An Interim Account

If we were to convey the essence of Tables 1 and 2 in a single statement, it would be that, to obtain an inverse-intensity effect, at least some of the stimuli must fall within the mesopic range, that is, between about -2 and 2 log cd/m^2. In greater detail, the salient inferences can be summarized as follows:

1. To obtain an inverse-intensity effect, at least some of the intensity levels must fall within the mesopic range. This is true whether we vary the intensity of the stimuli or the intensity of the background. The pertinent empirical evidence is summarized in the top portions of Tables 1 and 2.
2. When stimuli of varying intensity are displayed on a background of fixed intensity, an inverse-intensity effect is not found if the intensity of the background exceeds a critical level. It is possible that the critical level may depend jointly on stimulus and background intensities, such that no inverse-intensity effect is obtained if the combined intensities exceed the upper limit of the mesopic range. The empirical evidence is summarized in the lower portions of Tables 1 and 2.

At a first approximation, the relationship between intensity and persistence can be expressed in the following conjecture: If persistence is assumed to be constant and long at scotopic levels (below about -2 log cd/m^2), to be constant and brief at photopic levels (above about 2 log cd/m^2), and to vary smoothly between these two asymptotes in the mesopic region, then a good part of the experimental evidence in Tables 1 and 2 can be explained. This conjecture is represented graphically in Figure 1. We point out that the function in Figure 1 was not inferred from the data in Tables 1 and 2; rather, it was derived from a model of luminance discrimination and flicker perception proposed by Sperling and Sondhi (1968). A description of how the function in Figure 1 was derived from Sperling and Sondhi's model is given later in this article. But first, a procedural issue needs to be clarified. The experiments in Table 1 used variable-intensity stimuli on fixed-intensity backgrounds; the reverse was true for the experiments in Table 2. If the function in Figure 1 is considered strictly an empirical abstraction, devoid of theoretical implication, then it can be applied indifferently to both sets of data. As noted above, however, the function was actually derived from Sperling and Sondhi's model, which dealt with only the case of fixed stimuli on backgrounds of different intensities. In this theoretical context, the function in Figure 1 can be applied directly to the experiments in Table 2, but further argument is required to apply it to the experiments in Table 1. This argument is presented later in this article, when the Sperling and Sondhi model is discussed in detail. Here, our interest lies solely in establishing the validity of the function as an empirical descriptor of the relationship between intensity and persistence revealed in Tables 1 and 2 and summarized above.

An inverse-intensity effect is clearly discernible in Figure 1: The duration of visible persistence decreases markedly as lumi-

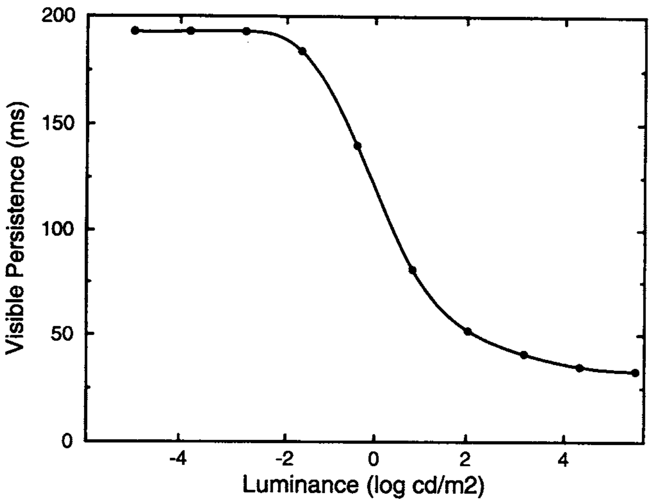

Figure 1. Estimated duration of visible persistence for small, brief pulses superimposed on backgrounds of varying intensities. Each point corresponds to the duration of the positive response of Sperling and Sondhi's (1968) model at the level of 20% of the peak amplitude, as indicated by the segmented line in Figure 3. Changes in background luminance affect the duration of visible persistence only in the middle range from about 10^{-2} to 10^{2} cd/m^{2}, corresponding to the mesopic range of vision.

nance level is increased. The effect of luminance, however, is most prominent at an intermediate range of values corresponding to the mesopic range. Differences in luminance at lower or higher levels affect persistence little, if at all. The manner in which specific levels of intensity are brought about (e.g., by different steady backgrounds or by brief stimuli on steady backgrounds) is not regarded as a major determining factor. Rather, what is important is the choice of luminances. For example, suppose that two stimuli differ in luminance by 1 log unit. Whether an inverse-intensity effect is obtained depends on where the two stimuli fall along the abscissa in Figure 1. A difference of 1 log unit produces a substantial inverse-intensity effect at intermediate levels of luminance but not at higher or lower luminances where the function is asymptotic. This is not to say that the specific luminance values shown in Figure 1 will necessarily apply in all types of displays and in all experiments; indeed, in some cases the level of retinal illuminance cannot be reconstructed with certainty from the published report. However, in any given experimental situation, it is to be expected that an inverse-intensity effect will be found at intermediate ranges of luminance but not at extreme ranges.

The function in Figure 1 provides a good match to the pattern of results summarized in Tables 1 and 2. Consider first the data in Table 1: In all experiments that obtained an inverse-intensity effect, the background was dark or dim and the range of stimulus luminances extended into the middle range, thus illustrated in Figure 1. By contrast, in most experiments that obtained no intensity effects, relatively bright stimuli were displayed on bright backgrounds, thus approaching the luminance levels at which the function in Figure 1 becomes flat. The study by Farrell et al. (1990) is no exception because, even though the background was dim, stimulus intensities were high and fell within a narrow segment of the function in Figure 1, where changes in intensity produce very small corresponding changes in duration of visible persistence.

Additional comments are needed to qualify other results listed in Table 1. In Wilson's (1983) study, stimulus intensity had no effect on performance in the case of "appearances" (i.e., if new dots making up a bigram were added to a background of existing noise dots). However, a direct-intensity effect was found in the case of "disappearances" (i.e., if some dots making up a bigram were turned off from the background of existing noise dots). The reason for this difference is unclear. In the study of Hogben and Di Lollo (1985), an inverse-intensity effect was obtained with different background intensities but not with different stimulus intensities, even when background intensity was low. This could have been due to a large increment in stimulus intensity brought about by spatial summation on the screen. The stimuli were dots displayed in rapid succession on an oscilloscopic screen to produce apparent motion. At small interdot separations, there was a good deal of spatial overlap between successive dots. In turn, spatial overlap produced stimulus intensities far in excess of the nominal values, perhaps shifting the actual luminances to the asymptotic part of the function in Figure 1. Whether this was, in fact, the reason for the absence of an inverse-intensity effect remains to be determined empirically. Finally, we omitted the study by Kinnucan and Friden (1981) from Table 1 even though it investigated the role of intensity in visible persistence. The study involved temporal integration of two sequential frames that could be of the same or different intensities. An inverse-intensity effect was found with ratings of simultaneity but not with accuracy measures. In addition, a significant interaction effect was found between stimulus-onset asynchrony and luminance. Interpretation of the results in the mixed-intensity conditions is further complicated by the effects of brightness mismatch with attendant forward and backward masking.

Expectations on the basis of Figure 1 also agree remarkably well with the data in Table 2. The range of background intensities used in studies in which an inverse-intensity effect was obtained spans the middle range of the function in Figure 1, where moderate changes in intensity bring about large changes in duration of visible persistence. The only study in this category that failed to find an effect of background intensity (Adelson & Jonides, 1980) used combinations of stimulus and background intensities clustered beyond 2 log cd/m^{2}, where the function in Figure 1 becomes flat.

A word of caution is required. There is little question that the tasks listed in Tables 1 and 2 make use of visible persistence as a source of information. It would be misleading, however, to assume that all those tasks rely exclusively on visible persistence. Instead, some tasks are performable on the basis of other sources of information that are less affected by intensity manipulations. The partial-report task with alphanumerical stimuli is a case in point. There is evidence to suggest that this task gives rise to at least two representations: one visible, the other nonvisible (Phillips, 1974; Sperling, 1967; Turvey, 1978). The first representation consists of visible persistence, similar to that produced by other types of stimuli, and responsive to intensity manipulations. For alphanumerical stimuli, additional processing time is required beyond the termination of visible persistence to decode and interpret the contents of the display. This processing activity gives rise to a second representation, which, although based on visual information, is nonvisible and is unaffected by stimulus intensity provided that the displays exceed visibility threshold. This representation has been denoted as "nonvisible trace" (Sperling, 1967), "informational persistence" (Coltheart, 1980), "nonvisual identity code" (Irwin & Yeomans, 1986b), and "schematic persistence" (Phillips, 1974; Turvey, 1978). Formal models of the relationship between the two representations have been proposed by Irwin and Brown (1987) and by Di Lollo and Dixon (1988). The distinction between visible and nonvisible representations is important because, with items requiring higher level processing, the partial-report task can be performed by making use of information in the nonvisible representation. Because the duration of the representation is not affected by stimulus intensity, an inverse-intensity effect should not be expected. This could be an additional reason that an inverse-intensity effect was not obtained in the study of Adelson and Jonides (1980). Related considerations played a part in other studies that revealed direct-intensity effects, to which we now turn.

Direct Intensity Effects

In examining the empirical evidence pertaining to direct-intensity effects, one must first identify a group of studies that showed improved *performance* with increased intensity of stimulation but not increased *visible persistence.* On occasions, these studies have been regarded as instances of direct-intensity effects in duration of visible persistence (e.g., Nisly & Wasserman, 1989). In fact, they cannot be regarded as such.

Perhaps most illustrative is the experiment reported by Keele and Chase (1967). A circular array of 10 alphanumerical characters was displayed briefly at one of three levels of intensity, followed by an arrow probe after an ISI between 0 and 5,000 ms. Accuracy of performance was found to be best at the highest intensity and poorest at the lowest intensity. However, this cannot be taken as evidence of a direct-intensity effect in duration of visible persistence because the differences in performance were present even at ISI = 0. This rules out visible persistence or *iconic memory* set as a factor. In other words, intensity made a difference even when the array and probe were temporally contiguous and, therefore, there was no ISI to be bridged by the icon. It follows that the direct-intensity effect was due to factors other than a longer lasting icon. A plausible option is that performance improved because the items became more visible—or more discriminable of one from the other—at higher intensities. For example, the letters *E* and *F*, which might be confusable at low levels of illumination, would become more discriminable at higher levels, and accuracy would improve. The same can be said for a study by Di Lollo and Woods (1981, Experiment 3) in which a direct-intensity effect was obtained at the shortest ISI (15 ms). At this ISI, the two sequential displays were seen as simultaneous when luminance was low (indicating adequate duration of visible persistence), but crucial details were hard to see, so performance suffered in comparison to higher luminances. In the same vein, the direct-intensity effect found in a partial-report study by Long and Sakitt (1980) cannot be ascribed unambiguously to duration of visible persistence because the intensity effect was present at ISI = 0.

Visibility of the stimuli, rather than duration of visible persistence, was also the likely determining factor in Long and McCarthy's (1982a) study in which 8 alphabetical characters were flashed at one of five levels of intensity between −0.5 and 1.5 log cd/m^2. Both whole reports and partial reports (to a dot probe at ISIs of 50 or 300 ms, respectively) were obtained. Accuracy of performance was found to improve markedly with intensity. Again, this cannot be taken as evidence for a direct-intensity effect in duration of visible persistence for at least two reasons. First, ISI had no noticeable effect on performance. Second, and more important, higher intensities produced better performance not only in a partial report (where longer visible persistence might have helped in bridging ISI) but also in a whole report where there was no ISI to be bridged. A more plausible account of this pattern of results is in terms of improved visibility of the stimuli at higher intensities.

Increased visibility is also the most plausible account of the results obtained by Sakitt (1976a) in a whole-report study. At the lowest stimulus intensity (−0.5 log cd/m^2), dark-adapted observers were unable to report any of the 12 alphabetical characters in the display, but performance improved rapidly as intensity was increased. A straightforward account can be given without recourse to iconic memory or visible persistence: The improvement in performance was obviously brought about by improved visibility of the stimuli as intensity was increased beyond visibility threshold. A second factor might have been at work in the study, especially at the higher stimulus intensities, which ranged up to 7 log cd/m^2. When stimuli of such a high intensity are delivered to dark-adapted observers, long-lasting retinal afterimages are produced (see J. L. Brown, 1965a). Such retinal afterimages must not be confused with visible persistence. The two are known to be distinct phenomena: They decay at different rates after stimulus offset, and their durations are affected in opposite ways by stimulus intensity and stimulus duration (Di Lollo, Clark, & Hogben, 1988). The direct-intensity effect obtained in Sakitt's study was ascribed to longer icons; yet, there is little doubt that performance with the brightest stimuli must have been mediated by retinal afterimages. Indeed, it has been suggested that retinal afterimages may have played a significant role in many instances of direct-intensity effects. This argument has been presented most cogently by Adelson and Jonides (1980) and by Bowling and Lovegrove (1982).

A combination of improved visibility at low intensities and retinal afterimages at higher intensities was clearly implicated in a study by Sakitt and Long (1978). In the study, observers were required to detect a gap between two rectangles displayed sequentially across a variable ISI at different levels of intensity. Performance was at chance at the lowest intensity, indicating that the displays were too dim to be seen. As stimulus intensity was increased, the displays became more visible, and performance improved correspondingly. Performance continued to improve as intensity was increased up to a level at which retinal afterimages lasting as long as 25 s were reported. The same two factors were almost certainly at work in another study by Sakitt (1976b) in which the intensity of the stimuli ranged from −2.95 to 7.5 log cd/m^2.

On inspection, it is clear that these and similar experiments are irrelevant to the issue of intensity effects in visible persistence. We reviewed them in some detail for the sole reason that, on some past occasions, they have been cited—inappropriately—as evidence for direct-intensity effects in duration of visible persistence. Next, we reviewed some studies—published mainly in the late 1970s and early 1980s—that could plausibly be regarded as evidence for direct-intensity effects in duration of visible persistence. Those studies (see Table 3) are closely related to one another and have been questioned—cogently and extensively—on conceptual and methodological grounds by several researchers (Adelson & Jonides, 1980; Banks & Barber, 1977; Bowling & Lovegrove, 1982; Di Lollo, 1983, 1984; Irwin & Yeomans, 1986a).

Over half the studies listed in Table 3 share the method of *synchrony judgments.* In this method, the observer is presented with a sequence of two stimuli: the *test stimulus* (a visual stimulus whose visible persistence is to be estimated) and the *probe* (an auditory stimulus or a visual stimulus distinct from the test stimulus). The interval of time between the offset of the test stimulus and the onset of the probe is varied from trial to trial, usually under the observer's control. To estimate the duration of visible persistence, the observer is required to synchronize the onset of the probe with the perceived termination of the test stimulus. In many of the studies by Long and colleagues (e.g., Long & McCarthy, 1982b), observers were required to make two separate types of synchrony judgments. In one type of judgment (*subjective offset*), observers were required to synchronize the onset of the probe with the earliest perceivable evidence that the test stimulus had been turned off (perhaps evidenced by a dimming of the display). In the second type of judgment (*fading trace*), observers were required to synchronize the onset of the probe with the complete disappearance of the last vestige of visibility of the sensory trace of the test stimulus. The intent was to illustrate two (or more) different processes underlying iconic memory.

Despite its intuitive appeal, this method is known to yield variable results and to be difficult to implement, regardless of sensory modality (e.g., Efron, 1973). The major difficulty is that the sensory trace does not disappear abruptly but decays gradually. This makes it difficult for an observer to set up and maintain a stable response criterion. In fact, this method has been criticized by many researchers (including Long, 1980) for being highly sensitive to shifts in response criterion. The problem is not limited to shifts in criterion *level;* there is reason to believe that criterion *content* can also vary. It has been pointed out that stimulus attributes other than visibility and processes other than sensory coding—notably, cognitive processes—can also play a role (Allan, 1979; Turvey, 1978).

An example illustrates this issue. In a study by Long and McCarthy (1982b; see Table 3) observers made two types of responses to the subjective offset of a visual stimulus: the reaction time (RT) and synchrony judgment with a trailing auditory probe. The results are illustrated in Figures 1a and 1b in Long and McCarthy's article. If the two figures are superimposed, a paradoxical result emerges: The latency of RT is *shorter* than the synchrony measure. This result is paradoxical because the synchrony measure is supposed to indicate when the very first evidence of stimulus offset is registered in the visual system; it should provide the sensory signal for RT. In turn, RT should take considerably longer because of the additional motor programming and execution times that are required. On the face of it, Long and McCarthy's evidence would indicate that observers can make a motor response to the termination of a visual stimulus before having realized that the stimulus has terminated. It seems likely that the observers had problems with criterion level, criterion content, or both. One possibility is that synchrony judgments were made to stimulus offset but that RT might have been affected by signals arising from stimulus onset. Whatever the underlying problem, the validity of the results and the credibility of the conclusions are impugned.

Entirely consonant conclusions have been reached by Irwin and Yeomans (1986a), who stated that

> the "synchrony-judgment probe-matching" task is simply an unreliable method, highly sensitive to shifts in an observer's criterion, that sometimes produces inverse effects and sometimes positive. . . . If a task is known to produce ambiguous results, is there any reason to put much faith in it? We think not. (p. 228)

We concur. At the very least, we believe that results obtained with the method of synchrony judgments should be cross-checked with techniques known to be criterion free. One such technique is the temporal integration of form parts (e.g., Eriksen & Collins, 1967; Hogben & Di Lollo, 1974; Uttal, 1969, 1970) which—by definition—yields estimates of the total duration of visible persistence. When this technique is used, two general outcomes emerge. First, estimates of the total duration of visible persistence with criterion-free methods seldom exceed about 200 ms. This is in agreement with the synchrony judgments reported by Bowen, Pola, and Matin (1974) and by Efron

Table 3
Direct-Intensity Effects on Performance

Author	Background (log cd/m^2)	Stimuli (log cd/m^2)	Task
Long (1985)	−0.52 0.48 1.48	0 to 3	Synchrony judgments (target–probe)
Long & Beaton (1980)	1.23 1.71 2.01	as background	Category ratings of duration
Long & Beaton (1982, Exp. 1)	−0.47	0.53 1.01 1.71 2.01	Partial report
Long & Beaton (1982, Exp. 2)	−0.52 0.53 1.53 2.01	0.53 1.01 1.71 2.01	Partial report
Long & McCarthy (1982b)	1.23 1.71	as background	Synchrony judgments (target–probe)
Long & Sakitt (1981)	0.23 1.23 2.23	as background	Synchrony judgments (target–probe)
Sakitt & Long (1979, Exp. 2)	−2.02	0.54 0.86 1.17 1.27	Synchrony judgments (target–probe)
Ueno (1983)	dark	−1.7 to 1.4	Synchrony judgments (target–probe)
Wilson (1983)	1.08	1.43 2.19	Temporal integration of form parts

Note. Exp. = Experiment.

(1970) but not with the much longer estimates typically reported by Long (e.g., Long, 1985). Second, a direct-intensity effect has never been reported with criterion-free methods, unless it was produced explicitly by using stimuli of sufficient intensity to create retinal afterimages (e.g., Di Lollo et al., 1988).

Two additional studies listed in Table 3 should be discussed: Wilson (1983) and Ueno (1983). Wilson found no effect of the stimulus intensity in the case of appearances (i.e., when new dots in the form of a bigram were added to a background of existing noise dots). In contrast, a direct-intensity effect was found—though only at some ISIs—in the case of disappearances (i.e., when dots forming a bigram were turned off from a field of existing noise dots). These results are of potential interest because they may illustrate the roles of *on* and *off* responses in visible persistence. However, they are not immediately related to the studies listed in Tables 1 and 2, and they can hardly be regarded as providing decisive support for the existence of direct-intensity effects in duration of visible persistence.

In Ueno's (1983) study, total duration of the fading sensory trace produced by a brief flash from a glow-modulator tube was estimated using the method of synchrony judgment with a visual probe. For dark-adapted observers, duration of visible persistence was found to increase gradually with flash intensity up to about 1 log cd/m^2 and to increase sharply thereafter. Very long estimates (beyond 1,000 ms) were obtained at the highest luminance. Aside from possible response-criterion problems (see above), these results may have been affected to an unknown extent by retinal afterimages at the higher levels of stimulus intensity. This is not to say that the results must be ascribed entirely to response-criterion effects or to retinal afterimages. However, until these potentially confounding factors are removed with appropriate methodologies, Ueno's results cannot be regarded as unambiguous estimates of the duration of visible persistence.

Is there a direct-intensity effect in duration of visible persistence? If no distinction is made between visible persistence and retinal afterimages, the answer must be in the affirmative. However, such a conclusion would be trivial. There is little doubt that, at intensities beyond the minimum required to produce retinal afterimages, the duration of the afterimage is related directly to intensity of stimulation (J. L. Brown, 1965a; Sakitt, 1976a). However, as noted above, visible persistence and retinal afterimages are different phenomena, easily separable on multiple dimensions. Taking into account only visible persistence, it must be concluded that the empirical evidence for a direct-intensity effect is far from convincing.

Related Effects: Flicker Fusion and Two-Pulse Threshold

In addition to studies aimed explicitly at visible persistence, there is rich experimental literature on two-pulse discrimination and flicker fusion that bears directly on the inverse-intensity effect. In such studies, the stimuli are displayed in temporal sequence at a fixed spatial location. In some instances, periodic stimuli of varying luminance are displayed on a background of fixed luminance (e.g., van Nes & Bouman, 1967); in others, the luminance of the background is varied. In either case, CFF is found to vary directly with stimulus luminance over a substantial part of the range. This is equivalent to an inverse-intensity effect in the temporal domain.

We propose (a) that visible persistence, the two-pulse threshold, and CFF are different manifestations of the same phenomenon and (b) that their dependence on stimulus intensity (the inverse-intensity effect) is based on common underlying principles and is explainable within a single conceptual framework. Establishing conceptual links among these three phenomena is not a new idea. Over a decade ago, Uttal (1981) affirmed: "I propose here that [two-pulse threshold and CFF] are not only conceptually identical but also attributable to the same underlying mechanism—response persistence" (p. 554). Perhaps the most convincing evidence of communality is that intensity manipulations affect CFF and two-pulse discrimination in much the same way as they affect visible persistence. In every case, the relationship between intensity and persistence can be portrayed by the same function, namely the function in Figure 1. To be sure, the fact that the function in Figure 1 can account for intensity effects in CFF is hardly surprising; as noted above, the function was derived from a model (Sperling & Sondhi, 1968) that had been explicitly aimed at explaining inverse-intensity effects in CFF.

Inverse-intensity effects in studies of flicker perception and two-pulse resolution have been well documented empirically (Boynton, 1972; J. L. Brown, 1965b; Kelly, 1972; Roufs, 1963, 1972a) and have been extensively modeled (Graham & Hood, 1992; Kelly, 1972; Roufs, 1972b; Sperling & Sondhi, 1968). These models are conceptually similar to one another and provide excellent accounts of the empirical evidence. For these reasons, this exposition is limited to a few examples.

Early instances of the inverse-intensity effect in flicker perception were reported by Charpentier (1887) and by Piéron (1922). Perhaps the best known example has been reported by Hecht and Verrijp (1933) and is reproduced in Figure 2. In comparing the data in Figure 2 with the theoretical function in Figure 1, one should keep in mind the reciprocal relationship between the frequency and temporal domains: Lower critical frequencies in Figure 2 correspond to longer durations of visible persistence in Figure 1. In agreement with the function in Figure 1, the data in Figure 2 show CFF to change most rapidly at a middle (mesopic) range of retinal illuminances. At lower and higher ranges, the effect is much smaller. Indeed, increments beyond about 3 log td (2.2 log cd/m^2) are seen to produce a decrement in CFF in Figure 2; in the temporal domain, this is equivalent to longer visible persistence. Thus, the inverse-intensity effect obtained in the middle range turns into a direct-intensity effect at higher illuminance values. This result is referred to later in connection with the role of photoreceptors in direct-intensity effects.

Essentially the same pattern of results is found in studies of two-pulse resolution. Intensity of stimulation has the greatest effect at a middle range of values. Studies reported by Kietzman (1967) and by Lewis (1967) illustrate this relationship. In both studies, two-pulse resolution thresholds were obtained from dark-adapted observers as a function of stimulus luminance. The outcomes of the two studies, however, differed dramatically. A strong inverse-intensity effect was obtained by Lewis: The duration of the temporal gap required to resolve two sequential pulses decreased progressively as stimulus luminance was in-

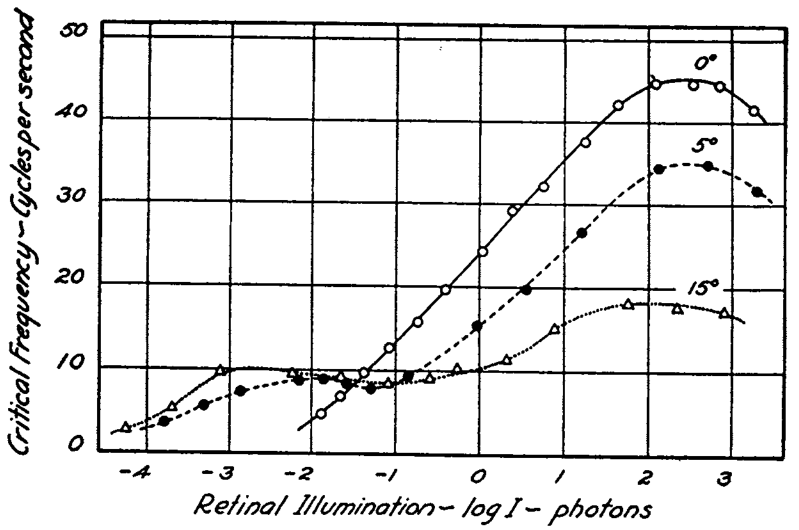

Figure 2. Critical frequency at fusion as a function of retinal illuminance for white light at three retinal eccentricities. (From "Intermittent Stimulation by Light. III. The Relation Between Intensity and Critical Fusion Frequency for Different Retinal Locations" by S. Hecht and C. D. Verrije, 1933, *The Journal of General Physiology, 17,* p. 257; Figure 2. Copyright 1933 by Rockefeller University Press. Reprinted by permission.)

creased. This suggests that the duration of visible persistence of the first pulse decreased as luminance was increased. By contrast, Kietzman found only marginal evidence for an inverse-intensity effect in one experiment and no evidence at all in a second experiment.

These contrasting outcomes can be reconciled by relating the luminance values used in the two studies to the function in Figure 1. The luminance values in Lewis's (1967) study were 0.008, 0.5, 1.5, 2.5, and 3.5 log cd/m^2. These values span a portion of the function in Figure 1, where changes in luminance lead to pronounced changes in duration of visible persistence. By contrast, the luminance values used by Kietzman (1967) were 2.1, 2.9, 3.3, and 3.5 log cd/m^2. These values cover a much narrower range and are crowded within a segment of the function in Figure 1, where changes in luminance produce very small corresponding changes in duration of visible persistence.

A specific aspect of the results obtained by one of Lewis's (1967) two observers deserves special notice. Duration of the critical interpulse gap decreased progressively as luminance was increased from 0.008 to 2.5 log cd/m^2. However, a further increment in luminance to 3.5 log cd/m^2 produced an *increment* in duration of critical gap. This is reminiscent of the effect found with flicker perception (Figure 2): The inverse-intensity effect seen at a middle range of luminance values can turn into a direct-intensity effect at higher values.

To recapitulate, studies of flicker perception and two-pulse resolution (see reviews by Boynton, 1972; J. L. Brown, 1965b; Kelly, 1972) provide clear support for an interpretation of inverse-intensity effects in broadly the same terms as the equivalent effects in visible persistence. In addition, there is evidence for direct-intensity effects in both CFF and two-pulse discrimination at high levels of luminance. As is explained below, such direct effects may be indicative of processes underlying similar effects noted in studies of visible persistence.

A Common Explanatory Basis

It is clear from the preceding review that the bulk of the evidence on the inverse-intensity effect can be explained in terms of the function in Figure 1. Thus far, the function has been treated merely as an expedient means of representing the empirical relationship between intensity and persistence, as revealed in Tables 1 and 2. In actuality, and as mentioned earlier, the function was obtained from a model of luminance discrimination and flicker detection proposed by Sperling and Sondhi (1968). Our choice of model was influenced to a large extent by the supposition that CFF, two-pulse discrimination, and visible persistence share common underlying mechanisms. If this were so, then a model capable of explaining intensity effects in the first two phenomena should also account for intensity effects in the third. Among several alternatives (Graham & Hood, 1992; Kelly, 1971a, 1971b; Roufs, 1972a, 1972b; Sperling & Sondhi, 1968), we selected the model of Sperling and Sondhi because it had been used successfully to account for CFF and had been used as a basis for modern elaborations by Graham and Hood. We wanted to show that a relatively simple, single-channel model such as Sperling and Sondhi's could be extended with minimal assumptions to account for the body of data on visible persistence.

It was not our intent to decide which of the possible alternative models provided the best account of the empirical evidence: In fact, this would not have been possible, given the nature of the data. The studies in Tables 1 and 2 differ widely in respect to such crucial variables as spectral composition of the displays—both spatial and chromatic, stimulus configuration, eccentricity, and experimental task. As noted earlier, not even the level of retinal illuminance could always be reconstructed with certainty from some of the published reports. Nor was it our intent to expand the scope of Sperling and Sondhi's (1968) model, as was done by Graham and Hood (1992), or to find new ways of estimating the impulse-response function of the visual system (Tyler, 1992). Our intent was simple: We used Sperling and Sondhi's model in its original version as a vehicle for explaining intensity effects in visible persistence.

Sperling and Sondhi's (1968) Model

Early stages of visual processing have been modeled in terms of cascading resistance-capacitance (RC) stages that are either entirely linear or contain feed-back or feed-forward connections (Fuortes & Hodgkin, 1964; Graham & Hood, 1992; Ives, 1922). Directly related to this tradition is the model of luminance discrimination and flicker detection proposed by Sperling and Sondhi (1968). The model consists of an initial cascade of two feed-back, one feed-forward, and six low-pass stages, followed by a decision stage. As Sperling and Sondhi pointed out, predictions from their model provide a good fit to the experimental data on flicker detection (e.g., De Lange, 1958) and can encompass the Ferry–Porter law. Sperling and Sondhi provide a detailed description of the components, and we do not need to repeat them. In our implementation, we used precisely the same equations and parameters that Sperling and Sondhi (1968, pp. 1134–1136) used. What is important is to determine how the system's output (i.e., the impulse-response function) varies as a function of input intensity. A family of response functions is needed that represent the system's output at different levels of intensity of the input. To this end, we implemented a computer simulation of Sperling and Sondhi's model and produced the family of curves in Figure 3, which are equivalent to the curves in Figure 7 in Sperling and Sondhi's article. The curves in Figure 3 represent separate visual responses produced by the system in response to brief pulses of light superimposed on backgrounds of different luminances. The curves have been normalized, as was done by Sperling and Sondhi. Normalization captures the action of adaptive processes, which permit the system to function optimally within a narrow range of intensities centered around adaptation level (Craik, 1938; Walraven, Enroth-Cugell, Hood, MacLeod, & Schnapf, 1990).

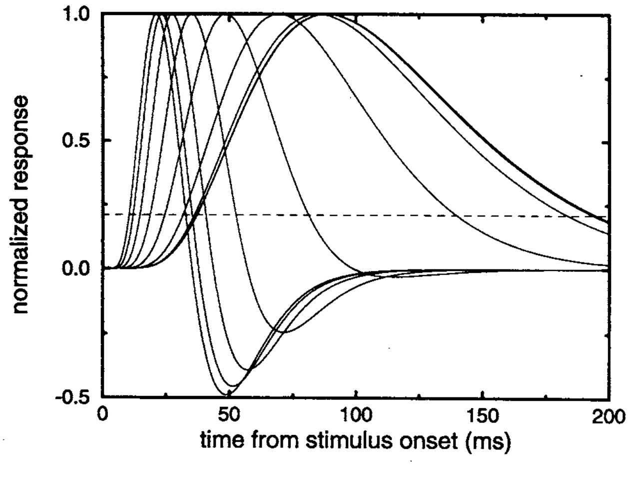

Figure 3. Normalized responses of Sperling and Sondhi's (1968) model to small, brief impulses superimposed on backgrounds ranging in luminance from about $2*10^{-5}$ to about $2*10^{5}$ cd/m^2. Successive background luminances differ by a factor of 10. The monophasic response with the longest time constant corresponds to the lowest background luminance; the biphasic response with the shortest time constant corresponds to the highest background luminance. The segmented line at 20% of the normalized peak amplitude was used for constructing Figure 1. Figure 3 is the same as Figure 7 in Sperling and Sondhi, but the data were computed independently.

Portrayed in Figure 3, the relationship between adaptation level and system responses may not be intuitively obvious or readily understood. Some elucidation is in order. Suppose that a small disk of light is presented for 10 ms to a light-adapted observer. Such stimulation triggers a series of changes in the level of neural activity for a period that can extend over several hundred milliseconds. At first, there is a positive phase, during which activity rises above background level. This phase is followed by a negative phase, during which activity drops below background level. Changes in activity such as these are described by the *temporal impulse response function.* The output of Sperling and Sondhi's (1968) model is akin to an impulse response function, although some differences do exist because of the nonlinearities inherent in Sperling and Sondhi's system. An example of the response produced by Sperling and Sondhi's model to a brief, low-intensity stimulus can be seen in the leftmost curve of Figure 3: The positive phase begins soon after stimulus onset; the negative phase ensues some 30 ms later, followed by a recovery to the level of background activity, represented by a value of zero. The salient difference among the curves in Figure 3 is the luminance of the background on which the notional stimuli were displayed. In turn, background luminance sets the system's level of light adaptation. The leftmost curve represents the brightest background; the rightmost, the dimmest.

Positive and negative phases of the temporal impulse response function represent excitatory and inhibitory visual processes, respectively. In this context, two aspects of the curves in Figure 3 must be noted. First, as background luminance is decreased, the size of the negative phase diminishes and eventually vanishes at the dimmest backgrounds. Lack of a negative phase in the dim background functions is consistent with the finding that, in scotopic vision, inhibitory processes are weak or absent (Ikeda, 1965; Kelly, 1971a, 1971b; von Békésy, 1968). Second, and more important for our purposes, the duration of the positive phase increases as background luminance is decreased. For example, the leftmost curve crosses the zero-level some 30 ms after stimulus onset; by contrast, the curves for the dimmest backgrounds are still above zero after 200 ms.

Predictions From Sperling and Sondhi's (1968) Model

Duration of visible persistence as a function of background intensity can be estimated from the functions in Figure 3, on the assumption that duration of visible persistence can be represented by the duration of the positive phase of the response function. This assumption is intuitively plausible because it relates the visibility of an image to the period of excitatory activity triggered by the physical stimulus. It is the simplest assumption linking persistence directly to the impulse-response function, and it has been used implicitly in several accounts of visible persistence (e.g., Farrell et al., 1990). Perhaps the most fitting justification, however, is pragmatic: Predictions on the basis of this assumption are confirmed nicely by the empirical evidence. On this assumption, estimates of the duration of visible persistence as a function of adapting luminance can be obtained directly from Figure 3. In obtaining these estimates, it was first necessary to define a threshold of visibility somewhere above the zero level. We selected an arbitrary level of 20%, indicated by the segmented line in Figure 3. We then estimated the duration of visible persistence for each of the 10 levels of background intensity represented by the 10 curves in Figure 3. This was done by determining the number of milliseconds that elapsed from stimulus onset to the point at which the relevant curve dipped below the threshold line. The resulting estimated durations of visible persistence are plotted as a function of luminance in Figure 1.

One last step is required if the function in Figure 1 is to apply equally to the data in Tables 1 and 2. Our argument is as follows: From a strictly empirical standpoint, the function in Figure 1 provides a good description of the evidence presented not only in Table 2 (studies in which stimuli of fixed intensity were displayed on backgrounds of varying intensity) but also in Table 1 (studies in which stimuli of varying intensity were displayed on backgrounds of fixed intensity). The differences between the two sets of studies become irrelevant if the function in Figure 1 is regarded strictly as an empirical abstraction from the data. It would simply show that the indicated relationship holds for intensity variations of either stimuli or background. If that function is derived from a model, as was done earlier, its applicability to both types of intensity manipulations cannot be merely assumed; it must be justified. To wit, the function was derived from the curves in Figure 3, which illustrate model responses to stimuli of fixed intensity displayed on backgrounds of varying intensity. So derived, the function in Figure 1 can account for only the evidence in Table 2. A question arises: Can Sperling and Sondhi's (1968) model also account for the evidence in Table 1?

First, the model must be capable of generating suitable families of responses made to stimuli of varying intensity displayed on fixed-intensity backgrounds. What is needed is a set of response functions similar to the curves in Figure 3 but obtained under conditions in which the luminance of the stimuli is varied systematically while the luminance of the background is fixed. Using our simulation, we generated model predictions over comprehensive ranges of intensities of stimuli displayed on backgrounds of fixed intensity. The outcomes of the simulation are illustrated in Figure 4. Each panel in Figure 4 represents a background of different intensity, ranging from dark (Panel A) to high photopic (Panel D). The response functions within each panel were produced by 10-ms pulses of light whose luminance was varied systematically as explained in the caption of Figure 4.

Two things should be noted in Figure 4. First, an inverse-intensity effect can be obtained by varying stimulus intensity. Second, background intensity sets a limit to the magnitude of the inverse-intensity effect. With reference to individual panels in Figure 4, the two effects can be described as follows. The curves in Panel A represent system responses to stimuli of varying intensity on a dark background. The leftmost curve corresponds to the brightest stimulus and the rightmost curve to the dimmest. The duration of visible persistence for each stimulus intensity can be estimated from the curves in Panel A in the manner described above: Namely, by determining the number of milliseconds that elapse from stimulus onset to the point at which the relevant curve dips below the visibility threshold indicated by the segmented line. On inspection, it is clear that duration of visible persistence varies inversely with stimulus intensity. If the estimates are plotted as a function of stimulus intensity, the resulting function is very similar to that in Figure 1, confirming the model's ability to account for the empirical evidence in Table 1. We argue below that these changes in duration of visible persistence are mediated by rapid light adaptation in response to different intensities of stimulation.

The effect of background intensity is seen in cross-panel comparisons. In Panel A the response functions show considerable spread along the time axis, indicating the importance of stimulus intensity as a determinant of visible persistence. The effect of stimulus intensity diminishes rapidly, however, as background intensity is increased. This is revealed by the progressive reduction in the spread of the response functions along the time axis from Panel A to Panel D. This effect, culminating in an absence of an inverse-intensity effect in Panel D, can be understood in terms of the function in Figure 1. The background luminance in Panel D corresponds to the high photopic levels at which the function in Figure 1 is flat; therefore, stimuli of different luminances cannot produce corresponding differences in duration of visible persistence.

We emphasize that the model offers a unitary account of the inverse-intensity effect, whether the intensity manipulations are performed on the stimuli or on the background. In either case, the inverse-intensity effect is explained in terms of a shift in the level of light adaptation with attendant change in the duration of the positive phase of the response function as illustrated in Figures 3 and 4. It is also worth noting that in the case of small, brief stimuli displayed on a fixed background (e.g., Table 1), the model makes two implicit assumptions. First, light adaptation at subbleaching intensities is rapid (in the order of milliseconds). Second, local retinal light adaptation can be induced by small stimuli in the order of minutes of arc. In a strict sense, the strongest justification for these assumptions is that model predictions that are implicitly based on such assumptions are confirmed by the experimental evidence. However, additional justification can be obtained from related experimental evidence.

The first assumption is well supported both empirically and theoretically. At low intensities (less than about 3 log cd/m^2), light adaptation is determined almost exclusively by neural processes taking place in retinal layers beyond the photoreceptors (Dowling, 1967; Hayhoe, 1990; Rushton, 1965). This is referred to as *neural light adaptation* to distinguish it from adaptation involving pigment depletion in the photoreceptors that occurs at higher luminous intensities. Neural light adaptation is fast: Hayhoe, Benimoff, and Hood (1987) estimated that it is accomplished in less than 50 ms. Koenderink, van de Grind, and Bouman (1971) provided a theoretical model of this mechanism and estimated its time constant to be on the order of 10 ms.

The second assumption is that light adaptation can be produced by small stimuli (in the order of minutes of arc) in small regions of the retina. For the rods, this assumption is well sup-

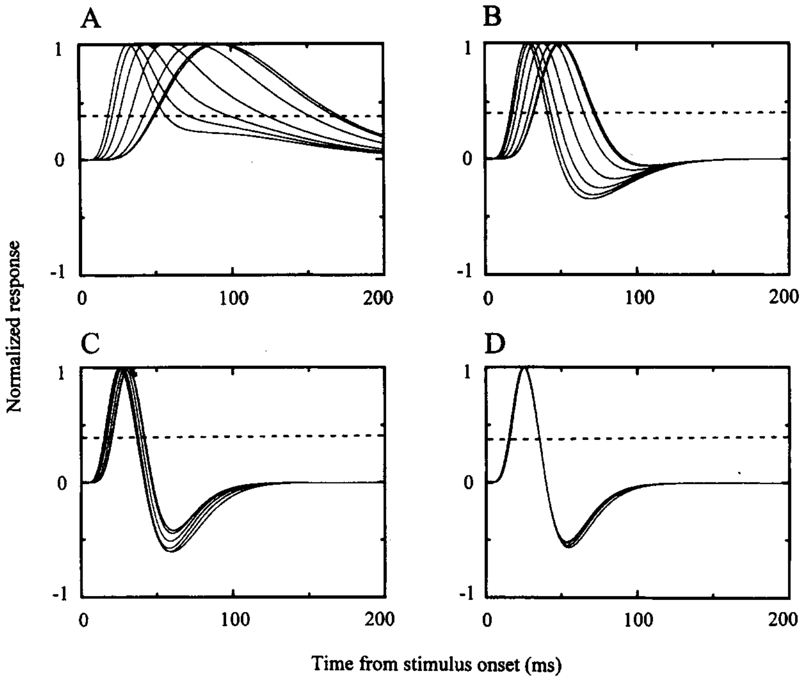

Figure 4. Responses of Sperling and Sondhi's (1968) model to brief (10 ms) pulses superimposed on background intensities of 0, 10^1, $10^{3.5}$, and $10^{5.5}$ cd/m^2 in A–D, respectively. Pulse intensities varied over ranges of 6, 7, 6, and 4 log units (in steps of 1 log unit) in A–D, respectively.

ported by Rushton's (1965) concept of "summation pools," each receiving input from many converging rods. MacLeod, Chen, and Crognale (1989) estimated the size of a pool at about 10 min of arc. As for the cones, MacLeod, Williams, and Makous (1985) found evidence for strictly local mechanisms of gain control, possibly residing in individual cones.

Taken together, the evidence shows that brief, small stimuli can induce rapid, local light adaptation. With reference to Sperling and Sondhi's (1968) model, this means that a small, brief input of sufficient intensity can produce an output with photopic response characteristics even if the system is initially dark adapted. In turn, the function in Figure 1 must be regarded as a valid description of the inverse-intensity effect, whether the effect is obtained with steady stimuli, with periodic stimuli, or with stimuli that are transient and brief.

Physiological Considerations

In his tutorial review of the literature, Coltheart (1980) suggested a possible neurophysiological mechanism for the inverse-intensity effect: inhibition of rod activity by cone activity. The account is based on two premises. First, rod activity decays more slowly than cone activity after stimulus offset. Supporting evidence for this premise has been provided by studies of late receptor potentials (Fain & Dowling, 1973; Whitten & Brown, 1973a, 1973b, 1973c). Second, at intensities above cone threshold, cone activity inhibits rod activity. Evidence in support of this premise has been adduced neurophysiologically with macaque monkeys (Whitten & Brown, 1973a) and psychophysically with human observers (Makous & Boothe, 1974; Stabell & Stabell, 1976).

Given these premises, explanation of the inverse-intensity effect is straightforward. At scotopic levels of luminance (below cone threshold), all ganglion cell activity originates from the rods, and the duration of visible persistence is correspondingly long (see the flat initial portion of the function in Figure 1). As luminance is increased to the mesopic range, responses are elicited from both rods and cones. However, as more cones become active, rod signals become increasingly inhibited. Conversely, as rods become dark adapted, there is less suppressive rod–cone interaction exerted by the rods (Naarendorp, Denny, & Frumkes, 1988). Taken together, both these factors act to diminish the duration of visible persistence (Figure 1, middle). Finally, at photopic levels, full activation of the cones inhibits all rod signals; at these intensity levels, ganglion cell activity originates only from the cones, and the duration of visible persistence is correspondingly brief (Figure 1, right).

Findings reported by Levick and Zacks (1970) confirmed the predicted temporal invariance of retinal responses as a function of stimulus intensity within the scotopic range. These investigators recorded responses of cat retinal ganglion cells to brief light pulses of varying scotopic intensities. It was found that response duration remained invariant (about 70–80 ms) within the scotopic range. However, substantially shorter responses were obtained when this range was exceeded. Levick and Zacks ascribed the reduction in response duration to the intervention of the cones at the higher level of stimulus intensity. As further evidence of cone intervention at the higher intensity, Levick and Zacks noted that the Purkinje shift is known to occur at comparable intensities (e.g., Barlow & Levick, 1968). It goes without saying that these results are entirely consonant with Coltheart's (1980) conjecture, as well as with the scotopic and incipient mesopic portions of the function in Figure 1. Essentially the same issue is addressed—albeit with some qualifications—by CFF curves in Figure 2. By and large, CFF (and, by inference, duration of visible persistence) remains invariant over a range of about 2 log units below a retinal illuminance of -1 log td. However, the generality of this finding must be qualified by a decrement in CFF at retinal illuminances below about -3 log td, which is still unexplained.

Homologous predictions regarding temporal invariance of retinal responses are made by both models in respect to stimuli at the photopic end of the intensity range. Predictions from Sperling and Sondhi's (1968) model indicate that intensity changes within the high-photopic range should have little, if any, effect on the temporal extent of the positive phase of the response function (Figures 3 and 4d); in turn, the inverse-intensity effect should be vanishingly small (Figure 1). Similarly, on the basis of Coltheart's (1980) conjecture, little if any inverse-intensity effect should be expected because, at high-photopic levels, all ganglion cell activity originates from the cones. As a corollary to these temporal invariances, neither model can predict the occurrence of direct-intensity effects at high-photopic levels.

On the face of it, these predictions seem to be at odds with the evidence of direct-intensity effects found at high-photopic levels. For example, the curves in Figure 2 show decrements in CFF (corresponding to increments in duration of visible persistence—a direct-intensity effect) at the highest levels of stimulation. A similar direct-intensity effect is evident in the two-pulse threshold of one of Lewis's (1967) observers at high-stimulus intensities. In general, direct-intensity effects have been obtained with high-intensity stimuli and dark-adapted observers in studies of CFF, two-pulse threshold, and duration of visible persistence (see Adelson & Jonides, 1980; Bowling & Lovegrove, 1982; J. L. Brown, 1965a).

In fact, these instances of direct-intensity effects are not at odds with theoretical predictions; they simply lie outside the scope of both Coltheart's (1980) and Sperling and Sondhi's (1968) models. This is so because the locus of the direct-intensity effects is almost certainly in the photoreceptor layer, whereas the processes modeled by Coltheart and by Sperling and Sondhi represent activity in retinal layers beyond the photoreceptors. The reasoning is as follows: The direct-intensity effects obtained in CFF and in related studies of two-pulse threshold and visible persistence strongly implicate bleaching of photopigment as the main mechanism of adaptation; in these studies, the switch from an inverse- to a direct-intensity effect occurred at about the levels (2.5–3 log td) at which rod photopigment begins to bleach in appreciable quantities (Campbell & Rushton, 1955; Cornsweet, 1970) and at which retinal afterimages of any consequence begin to emerge (Alpern & Barr, 1962). Clearly, these contingencies implicate the photoreceptor layer as the main adaptation site. This very site was explicitly excluded from the scope of both models. For example, Coltheart referred explicitly to horizontal and amacrine cells as the presumed sites of cone–rod inhibition. In the same vein, Sperling and Sondhi referred to their model as representing neural excitatory processes controlled by synaptic inhibition; photoreceptor modeling was explicitly ruled out. Future expanded versions of these models may well encompass photoreceptor processes and thus may be capable of accounting for direct-intensity effects at high-photopic levels. However, photoreceptor processes are outside the scope of both models as presently formulated.

Conclusions

Two themes are central to the present work. First, the inverse-intensity effect obtained with three separate perceptual events—CFF, two-pulse threshold, and visible persistence—can be encompassed within a single conceptual framework. Second, the inverse-intensity effect observed in all three phenomena can be explained in terms of the model proposed by Sperling and Sondhi (1968).

In developing these themes, we dealt extensively with visible persistence but only cursorily with CFF and two-pulse threshold. We opted for this approach because Sperling and Sondhi's (1968) model was already known to provide a satisfactory account of CFF and two-pulse threshold. In contrast, there was no extant systematic account of the experimental evidence on visible persistence. Having examined the evidence, we find that it agrees with theoretical predictions to a remarkable degree. In essence, the inverse-intensity effect is explained by the model of Sperling and Sondhi as instantiated in the predictions illustrated in Figures 3 and 4.

In the case of CFF and two-pulse threshold, the direct relationship between the intensity of stimulation and critical temporal frequency (i.e., inverse-intensity effect) had been established for some time and had been formalized in the Ferry–Porter law (see De Lange, 1954). Possibly because it was carried out within a separate traditional area of psychology, experimentation in visible persistence developed in relative isolation from experimentation in CFF and two-pulse threshold. Theoretical models also developed along different lines. Models of CFF have been couched mainly—though not exclusively—in the frequency domain within the tradition of linear-systems analysis (e.g., Ives, 1922; Kelly, 1972; Roufs, 1972b). By contrast, models of visible persistence have been couched principally in the temporal domain within the tradition of neurophysiology (e.g., Duysens, Orban, Cremieux, & Maes, 1985; Groner, Bischof, & Di Lollo, 1988). In view of the separate traditions, it is not surprising that Sperling and Sondhi's (1968) article was not cited in Coltheart's (1980) scholarly review.

In the present work, we have attempted to integrate the two traditions within a single, coherent account. In this context, Sperling and Sondhi's (1968) formal model and Coltheart's (1980) neurophysiological conjecture are shown to be compatible accounts of the inverse-intensity effect. Both accounts are supported by the empirical evidence in CFF, two-pulse threshold, and visible persistence. In a nutshell, whether the account is couched in mathematical or in neurophysiological terms, the inverse-intensity effect can be explained in terms of the mechanisms and processes of mesopic vision.

A retinal account of the inverse-intensity effect does not imply that visible persistence must be an entirely retinal phenomenon. Other attributes of visible persistence, such as its dependence on the spatial-frequency composition of the stimulus, implicate higher levels of visual information processing (Di Lollo & Woods, 1981; Meyer & Maguire, 1977, 1981). We believe that visible persistence, like many other visual phenomena, is not a unitary effect;

rather, as the coding of the initial stimulus proceeds from retinal to higher processing levels, concomitant short-lived representations might ensue, each stemming from—and coded in terms of—the prevalent processing activity taking place at a given stage. In terms of this multidimensional conception, different attributes of visible persistence are related to coding activities at separate loci and processing stages. In the case of the inverse-intensity effect, the evidence suggests that the locus of the salient processing stage is in the retina.

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